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JANUARY, 1946

No. 1

Dispersion of Small Organisms

Distance Dispersion Rates of Bacteria, Spores, Seeds, Pollen, and Insects;
Incidence Rates of Diseases and Injuries

D. O. Wolfenbarger

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Preface

As has long been recognized, the distance dispersed by organisms has not only great scientific interest but is also very important in planning control measures. This double significance offers a challenge for quantitative research on dispersion of organisms. The present paper was prepared in an attempt to meet this challenge, at least in part. Imperfect as quantitative measures and methods may be, they provide nevertheless more complete understanding of already established qualitative knowledge. Furthermore, they permit probing for new concepts.

Acknowledgment is made to Dr. F. M. Wadley for encouragement to carry on this work, and for his many helpful suggestions in its preparation. To many unnamed entomological and other friends and associates thanks are given for permission to use certain unpublished data, and for suggestions in connection with the manuscript.

Introduction

That organisms disperse or are dispersed in one or more of their life stages is a common biological truism, for dispersal is essential to life in the propagation of the species. The process of dispersion for each stage, species, or other biological unit follows patterns or horizontal distance dispersion regardless of the methods, reasons, stages or other factors involved. An axiom of dispersion of organisms is that there is a reduction of biological units with an increase of distance from point of origin. The rate of reduction with distance increase, or regression is of great importance in many or most economic studies. A regression constant for each species, group, stage, phase, or activity would be a desirable and a valuable adjunct to the knowledge of each.

A preparatory review of the literature by Wadley and Wolfenbarger (1944) showed that not only insect dispersion and insect injury incidence but that seed, pollen, spore dispersion, and disease incidences also tended to follow linear relationships by plotting the dispersion or incidence data on semi-logarithmic scaled paper. This tendency was evident whether the organism dispersed actively or passively, mechanistically or teleologically. Quantitative data on horizontal distance dispersion of insects, seeds, spores, pollen, and disease or injury incidence distributions proved to be so few that the task of presenting them collectively was not too difficult.

Hundreds of books and periodicals have been examined to obtain the published records for this work. It is hoped that the more outstanding records, at least, have been obtained and utilized. The titles of papers, it was observed, often fail to indicate the presence of any dispersion or incidence data. Some papers, therefore, may have been overlooked. Only a very small portion of publications, particularly of the older ones, contains quantitative data on dispersion or incidences. During the last decade, however, an increase in quantitative data can be seen in such publications.

Tutt (1902) who was not satisfied with the question of insect migration and dispersion said it had, "... received nothing but the most haphazard

treatment . . .", but foresaw, "Already there are signs that scientific methods will be applied in the near future to this subject and that careful observations and reliable statistics will furnish data for useful generalizations bearing on the subject." It is hoped that this presentation may fulfill, in some measure at least, an object of more recent expression given by the Committee on Quantitative Ecology, Park (1941), that, "There is a creditable amount of work already existing here of a qualitative and descriptive nature but little that pictures dispersion in a quantitative and analytical fashion."

Care has been exercised in avoiding misinterpretation of authors' data. Any and all known published data, however, have been used freely to compute trend lines of dispersion and incidence. If the regression data were judged by statistical methods part of the reported observations would undoubtedly fail to be significant. No effort was made to evaluate and judge them in that manner.

Terms and Conceptions

The term "dispersion" does not have the same meaning throughout the literature. Synonymous meanings for the terms "dispersion," "migration," and "emigration" are frequently encountered. As these terms are employed in genetical, taxonomical, physiological, geographical, ecological or other contributions, their meanings are so diverse that some confusion is to be expected. The most commonly confused terms are "dispersion" and "migration." Clarifying discussions of the use of these terms are presented by Thomson (1929) and Clark (1931). The concepts presented by Heape (1931), however, are not synonymous with those discussed by Thomson (1929) and Clark (1931).

Dispersion of organisms is the going from one place to another, whether mechanistically or teleologically motivated, or whether the organism is self propelled or is propelled by energy from an outside source. It is usually considered as an uncontrolled movement, or meandering about without a definite location as a goal.

The term "migration" is considered to refer to movements between locations where breeding occurs at one or both locations. Migration is exemplified by many waterfowls and fishes, by movements between rather widely separated locations. These locations are generally, although not necessarily sought at the outset of the movement.

The term dispersion is used throughout the ensuing discussions. It is (1) generally accepted by usage, (2) applicable by definition, and (3) indicative of the processes involved. Since disease and injuries obviously cannot disperse but result from dispersion and since they too exhibit patterns symbolical of organismal dispersion, the term "incidence" is used in reference to them. Dispersion is here applied to the movements of a species or group through one generation, phase, stage, cycle, or activity and only data from a given cycle are included. For organisms from secondary or later cycles should be excluded from the primary movement, as they would initiate a new dispersion process. It is the term applied where the species has been long established or where it may be a factor in the distribution of the species in a new country. However,

following Tutt's (1902) example, no attempt is made in this treatise "... to enter here into the wide and general subject of the geographical distribution."

The broad, extensive and general subject of "distribution" is treated by many authors. The recent book by Cain (1944) and the earlier one by Willis (1922) are recommended as references.

The term "regression," frequently used in this contribution, literally means going back or retrogradation, reverting toward zero. The regression curve originates nearest the source of the organism and terminates furthest from the source. The slope or rate of fall of the curve illustrates the rate of dispersion. Although the regression curve draws toward zero organism at its termination there is a marked tendency to reach low levels and to decelerate to lower levels without reaching zero. The absence of organisms is reached at a more remote and unknown distance than the most remote distance observed.

Reduced numbers of organisms at increasing distances from the source are attributed to two principal factors, (1) spreading out over wider areas, and (2) stoppage of organisms, discussed briefly by Wadley and Wolfenbarger (1944). More extensive qualitative discussions are found in the works of Moulton (1942), Whitehead (1939), Fraenkel (1932) and Williams (1930). Data obtained by well designed and executed tests estimate the net results of movements whatever the factors may be or however they affect dispersion. It is desired to indicate, however, that considerations of both quantitative and qualitative dispersion observations are essential for a balanced program of research.

It may, and often is, impossible to learn the maximum distance of dispersion or incidence. Also, it may be, and often is, impractical to utilize the maximum or total dispersion or incidence of a species. Whitehead (1939) in emphasizing the importance of insect dispersion and disease incidence reported that, "Research may determine the normal flight of a species, but it will not take into account the accidental dispersion of that species due to abnormal climatic conditions, nor must the deliberate flight range of an insect be confused with the distance that the insect may, on occasion travel owing to wind drift." In a practical way Patch (1921) expressed a sound philosophy in saying that "We do not need to know how far an individual can fly, so much as we need to know how far . . . [the average, or some portion of them can disperse] . . . to be out of danger. . . ."

The distance from the source that dispersion or incidence may be employed for control purposes cannot be overemphasized. Studies of dispersion or incidence may indicate local control, as by an individual, or may point to other control as by an organization with wide jurisdiction, depending on the distance and other factors involved. The objective of an economic program is the utilization of some portion, for example 75, 95 per cent, or if possible the total dispersion or incidence.

Horizontal dispersion is one of two recognized types, the other type being vertical dispersion. The vertical distance an organism moves or is moved does not indicate its horizontal distance of movement. It is conceivable that an organism may disperse widely and distantly but remain near the ground surface

while it is doing so. There is some evidence which verifies this conception and is discussed under Generalizations. Relationships between the two types undoubtedly exist. Whatever the distance or abundance of vertical dispersion and its relationship with horizontal dispersion may be, the important type is horizontal since only those organisms which come to earth, or near to earth, in active or viable conditions are of significance.

Methods

Available reports giving quantitative results served as the source of material for illustrating the rates of dispersion and incidence. Only those papers were utilized which contained three or more comparative distance points with their corresponding dispersion or incidence data. In many papers these data were poorly organized for convenient or quick determination of the dispersion or incidence rates. In these cases and in papers in which some apparently irregular values were observed, it is hoped that trend lines, or regression curves will show rates of dispersion and incidence.

Methods previously described by Wadley and Wolfenbarger (1944) were used to compute values for plotting the curves. The formulae,

$$E = a + b (\log x), \text{ or} \\ E = a + b (\log x) + c (1/x)$$

were used for authors' data as indicated in the appendix. The "E" is for the expected, calculated, or theoretical value; "a" is the position on the graph; "b" and "c" are factors determining the slope of the curve as influenced by the logarithm or reciprocal of the distance. The methods suggested by Zentmyer et al. (1943, 1944), Frampton et al. (1942) and Stepanov (1935) were, however, given consideration. These references are discussed further on pages 17, 20, and 24.

Observed values from authors' data and calculated values were studied on graphs in which the x-axes, or distance units, were spaced logarithmically, and the y-axes, dispersed or incidence units, were spaced uniformly. Dispersion, incidence or other units converted to straight lines by this means have certain advantages over the curve line relationships portrayed on uniformly spaced grids. These are, (1) straight lines are more easily computed, (2) interpolations (and extrapolations) are more easily made, and (3) slopes of dispersion rates from different species, or the same species under different conditions are determined more readily. Dispersion or incidence units transformed to logarithmic or other units for computation of the regression line, followed by retransformation to the original type of unit may after retransformation depart somewhat from the original observed values.

The graphic method which has some advantages over other methods was chosen to show the comparisons. The original observations, by this method, may be quickly compared with the calculated or expected value. Furthermore, extrapolation of the curves, a rather risky procedure but suggestive of possibilities, may be considered, and interpolations may be made to assist in adjusting control practices. Distances converted to logarithms for calculating expected

numbers were converted again to the original values, however, in uniform spacings for the illustrations.

This contribution is divided into two principal parts. The regression curves of dispersion or incidence on distance, based on published sources are presented in Part I.

Generalizations of dispersion characteristics and functions are given in Part II. Part I is divided according to taxonomic groups, an arrangement followed by Glick (1939) Fraenkel (1932) and Tutt (1902), whereas Part II is divided according to principal topics.

Part I.—Dispersion and Incidence Rates

Horizontal Dispersion

Kingdom Inanimata

Water Splashes.—Wind-blown rain was believed by Faulwetter (1917) to be a very important factor as an agent of transmission for disease organisms. Experiments were conducted which illustrate distances to which water droplets splashed. Distances of droplet spatter were found to vary considerably, depending on volume, size of drop, and distance of fall before impact. Although considerable data were presented and several regression lines could be computed, figures from Faulwetter (1917, table 1) were used to calculate a regression curve (fig. 1A).

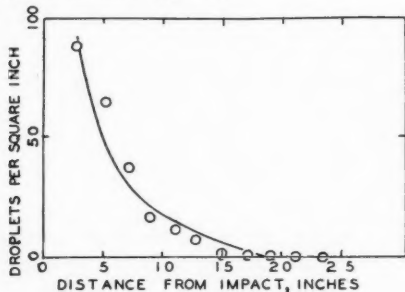


FIG. 1A.—Dispersion of water droplets (data from Faulwetter).

A low frequency of water droplets from splash fell at 17 inches from the point of impact. The maximum distance observed was considerably more remote, however, than 17 inches. The curve strikes zero at near 18 inches.

Data from Faulwetter (1917) are of further interest since they include the distance dispersed of various volumes from the source. Different volumes might be compared for distance dispersed as are different population levels of insects. For further discussion of this reference see Part II.

Balloons.—Balloon release studies, recorded in the entomological literature by Felt (1937), and Gaines and Ewing (1938) were made in order to further our knowledge of insect dispersion. The interest and considerations of these inanimate, inorganic objects with reference to insect, seed, spore, and pollen dispersion warrant their inclusion in this review.

The distance range of the data given by Felt (1937) was divided into ten distance class groups whose intervals were 20 miles. The number of balloons falling in each of these distance classes was then determined. From these data the rate of balloon dispersion was calculated (fig. 1B).

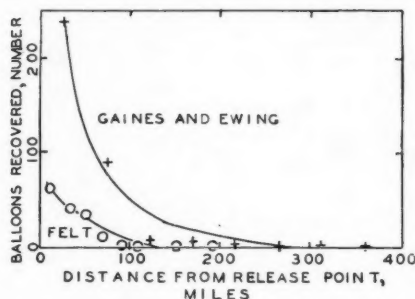


FIG. 1B.—Balloon dispersion (data from Gaines and Ewing, and from Felt).

Expected numbers of 63 and 5 balloons at distances of 10 and 110 miles, respectively, compare with observed numbers of 59 and 2 which indicates fair agreement of observed and calculated values. Zero, by computed numbers, was reached at near 130 miles. One balloon, however, was reportedly recovered in each of the 150 and 190 mile classes.

Considerable balloon dispersion data were summarized by Gaines and Ewing (1938) from their experiments in Texas. More details, however, were desired for computation of a curve. Through the kindness of these investigators more detailed data and information were made available.

The balloon recovery data were divided into eight distance classes, each 48 miles. The number of balloons falling in each distance class, regardless of the direction dispersed from the release point, was determined and is shown in Fig. 1B.

Within 48 miles 240.6, and between 240 and 288 miles 0.2 balloons were calculated to have fallen, while the observed numbers were 236 and 0. Zero recovery was reached, theoretically at near 265 miles. Two balloons, however, were recovered at distances greater than the computed zero. Agreement of the observed and calculated values lacks as close alignment as might be desired although there is no extreme variant.

Unidirectional dispersion toward the northern and northeastern direction is recorded in both of the above papers on balloon dispersion. The balloons used contained no inherent motive power aside from that to arise vertically, but depended on external forces for horizontal dispersion. The wind, or air currents, may be considered as the agent of dispersion, and, at the time the balloons were in suspension, to have had northern or northeastern directions. Organisms which depended partly or wholly on external forces for dispersion might be expected, therefore, to have been forced northward or northeastward. The use of balloons to indicate directional tendencies of passive disperser organisms is demonstrated. The effects of distance, or rates of balloon dispersion, however, cannot be expected to parallel those of organisms.

Kingdom Vira

The incidence of aster yellows in beds of lettuce and endive was studied by Linn (1940). The data from four beds were summarized in graphic form by the author, and are reproduced from the original (fig. 1C).

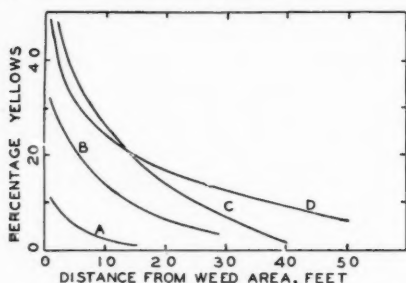


FIG. 1C.—Incidence of aster yellows [tracing from Linn (1940, fig. 9)].

Incidence of aster yellows, transmitted by the six-spotted leafhopper, *Macrosteles divisus* (Uhl.), is shown to be restricted to short distances near the margins. Two beds (C and D) whose initial incidences were more than 50 per cent had few diseased plants 50 feet from the margin. Two beds (A and B) whose initial incidences were near 13 and 37 per cent infected plants tended to reach zero per cent yellows at near 27 and 37 feet, respectively. The similarity of contours exhibited by these curves (fig. 1C) warrants further reference under Generalizations.

Studies on the incidence of curly top disease affecting sugar beets and other plants are given by Annand et al. (1932) and by Romney (1939). The data given by them show that diseased plants decreased as the distance from the leafhopper breeding grounds increased (fig. 1D).

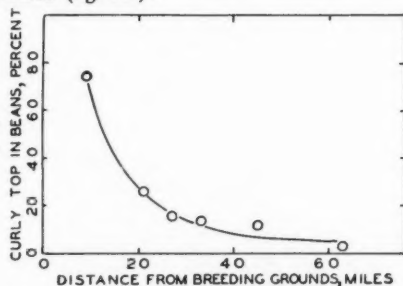


FIG. 1D.—Incidence of curly top disease on beans (data from Annand et al.).

Over one half of the bean plants within 12 miles of the breeding grounds of the beet leafhopper, *Eutettix tenellus* (Bak.), which transmits the curly top virus, are shown (fig. 1D) to be infected. Low levels of infections were reached at 60 miles from the breeding grounds. Low incidences of diseased plants existed at distances greater than 65 miles, the most extreme distance under observation.

Romney (1939) showed how in western Texas the percentages of sugar beets infected with curly top disease decreased with distance increase unidirectionally northward from the breeding grounds of the beet leafhopper, *Eutettix tenellus* (Bak.). Data covering five years for each of several distances were obtained. A statistical test of these data showed that years and distances differed significantly in the amounts of disease present. Results of the test provided justification for combining the data from the years of 1928 and 1929, of 1930 and 1931, and for separating the data of 1933 for three regression curves (fig. 2A).

Incidences of 100 per cent infections are shown at considerable distances from the overwinter breeding grounds of the beet leafhopper. The percentage of infected plants recorded in one year, 1933, by computed numbers, showed 100 per cent infections up to near 125 miles from the apparent source. Small percentages, less than 18, were shown at distances of 450 miles. Extreme distances of curly top incidence extends beyond 430 miles.

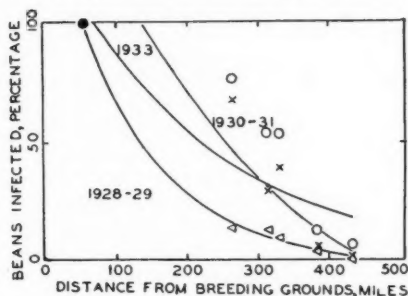


FIG. 2A.—Incidence of curly top disease on sugar beets (data from Romney).

This is an example of wide interstate disease incidence. Some form of Federal control to break up the sugar beet leafhopper populations at their source is suggested.

Incidence of potato yellow dwarf disease was shown by Frampton, Linn, and Hansing (1942) to be somewhat circumscribed about old meadows, source of the leafhopper, *Macrosteles divisus* (Uhl.), transmitting the virus. A regression curve was prepared to show the incidence rate (fig. 2B).

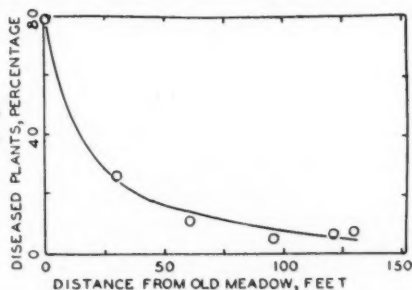


FIG. 2B.—Incidence of potato yellow dwarf disease (data from Frampton et al.).

Reductions of disease incidence to markedly lower levels are shown by 90 feet. Fluctuations in the percentage of diseased plants are seen at the 120 and 135 foot distances. These fluctuations, attributable to leafhopper dispersion from multiple sources, affected the curve by a flattening effect. A steeper curve seems likely if these multiple sources were eliminated. Effective and practical distances of 90 feet from old meadows offer a means of separating potato fields from sources of the leafhopper and a control of the disease.

Distribution studies of potato mosaic were made by Folsom, Schultz, and Bonde (1926) in fields planted to healthy potatoes adjoining fields with diseased plants. Percentages of mosaic infected plants were given for distances, in terms of rows, from the outside or marginal row to a distance of 712 rows from the margin. Considerable data from several fields were given, all of which were combined to show the average rate of disease infection decrease with distance increase.

The smoothed curve percentages of disease are 12.2 and 12.6 at the margin and 712 rows distance, respectively. This is very slight and is probably insignificant; no figure, therefore, is given. The distance range is too short to measure wide differences between even the most widely separated observed points.

Decreasing percentages of potato mosaic disease over a distance range of five rows from diseased plants, are shown by Murphy (1921) in his investigations of potato virus diseases. The percentages of infection for each distance class and locality (except two in which there were no data in some distance classes) were summed and averaged to show the average rate of disease decrease. The distance value of, "Between two rows" of contaminated plants was taken as of a unit distance nearer the inoculum source than, "Row next" (fig. 2C).

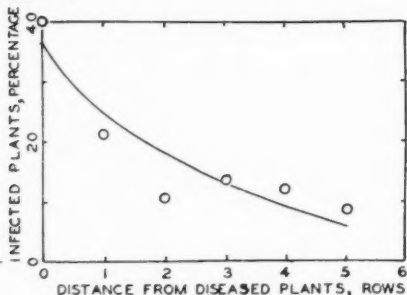


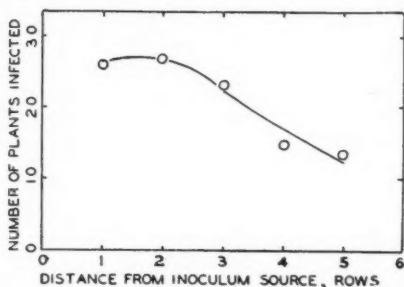
FIG. 2C.—Incidence of potato mosaic disease (data from Murphy).

Nearly one-fourth as many infected plants were found at five rows distance from as between two rows of diseased plants. This may be considered a fairly rapid rate of potato mosaic incidence. It may illustrate, for example, the effectiveness of roguing diseased plants from fields and how the practice is a control of the virus. Localities, as shown by the original data, exerted very marked influences on the incidences of mosaic contaminations; neighborhood infections varied from location to location and from year to year. Locality differences may account for some of the differences in the incidence rates calculated from data given by different authors. Such differences might explain

how a small difference existed between the extremes of the distance range reported by Folsom, Schultz, and Bonde (1926), reported above, compares with the wide differences over a much shorter distance range in Murphy's observations (fig. 2C). It is suggested that different insect population densities, discussed under Generalizations, may explain some locality differences, possibly even some between years.

A study of potato calico spread in field plots was reported by Porter (1935), in which data from 3 plots, each 11 rows long and 10 plants wide, were given. The middle one of the 11 rows was planted with seed pieces containing the calico virus, source of the inoculum. The five rows on each side of the virus harboring seed pieces were planted with seed pieces from healthy plants. The number of infected plants at the different row distances were used for drawing an incidence curve (fig. 2D).

FIG. 2D.—Incidence of potato calico spread (data from Porter).



Infected plants were less frequent in the more distant rows. Expected numbers of diseased plants were 26.1 and 12.8 at distances of one and five rows, respectively, from the source. Further reference is made to this example under Generalizations.

Doolittle (1925) showed how cucurbit mosaic symptoms appeared earlier on cucumber plants nearer overwinter harborers of the virus than on more distant plants. The data from the two years' results were combined and used to show the average rates of mosaic symptoms (i. e., 3A).

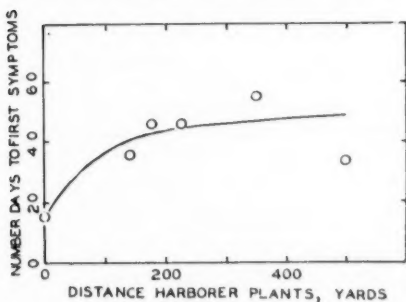


FIG. 3A.—Time incidence for cucurbit mosaic symptoms to appear (data from Doolittle).

A positive regression, or increase, of time for the first symptoms of mosaic with increase of distance is shown, as might be expected. The rate of increase, however, for the first symptoms is indicated by 16.6 and 48.7 days at 1 and 500 yards, respectively, according to computed numbers. It may be concluded from these data that the vectors inoculated the nearer plants first, or that the nearer plants received more inoculum which resulted in a shorter incubation period of the disease.

Rather extensive studies of celery mosaic were reported by Wellman (1935) (1937). It was shown that the relative numbers of infected plants were related to local distances from plants harboring the inoculum (fig. 3B).

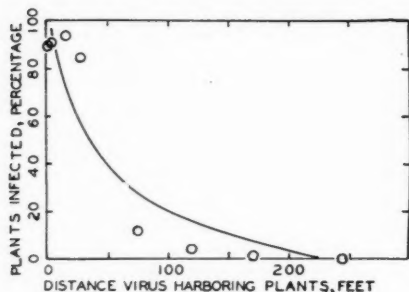


FIG. 3B.—Incidence of celery mosaic (data from Wellman).

Most mosaic infected plants were found within 100 feet of the virus-harboring aphid infested plants. Localized efforts to eliminate nearby plants appear practical and were recommended by the author. Zero infected plants were calculated to have been reached at near 225 feet from the inoculum source.

Proximity of wild brambles was shown by Cooley (1936) to have provided the source of severe streak in cultivated raspberries. From the author's figure 3 data were obtained by counting the number of diseased plants in a strip of rows across the field. This strip, or band, across the field began with the rows in the middle of the longest straight portion of the figure where the field adjoined the brambles and extended to the side of the field opposite the bram-

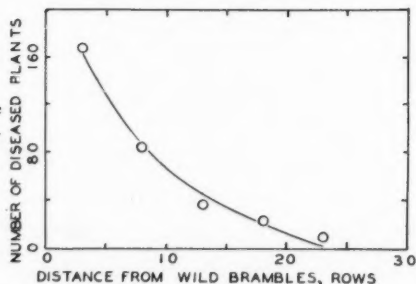


FIG. 3C.—Incidence of severe streak disease (data from Cooley).

bles. The strip was 20 plants wide and 25 rows long. The 25 rows were divided into five, five-row distance intervals to show the incidence rate (fig. 3C).

Most of the diseased plants were in the rows adjoining the wild brambles. There were 165 and 1 diseased plants at the midclass distance rows of 3 and 23, respectively, based on expected numbers. Fair agreement of observed and computed values is seen.

Incidence of potato spindle tuber infections was reported by Folsom, Schultz, and Bonde (1926). Mosaic infections reported above from Folsom, Schultz and Bonde (1926) and the data on spindle tuber were gathered from the same fields and at the same distances, from field margins to 712 rows away. The data from all fields were combined to illustrate the spindle tuber incidence (fig. 3D).

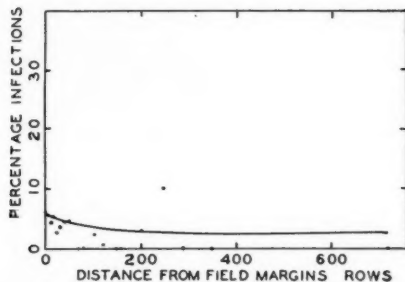


FIG. 3D.—Incidence of potato spindle tuber infections (data from Folsom et al.).

A slight decrease in the number of spindle tuber infections with increase in distance is indicated. The percentage of mosaic in the marginal row was 5.9 and in the 712th row was 3.4, based on expected numbers. The agreement of observed (not shown) and calculated values is more widespread than is desirable. Possibly the distance range may have been too short for measurement of widespread differences of spindle tube infections, as for potato mosaic.

Incidences of potato leaf roll disease were shown to vary in different provinces of the Dominion of Canada, according to Murphy and Worthley (1920). Potato seed pieces not contaminated with the leaf roll virus were planted between two rows of diseased plants, adjoining rows of diseased plants, and from two to five rows distant from diseased plants. These were given distance classifications of 1 to 6 row distances, which with the average percentages from the different localities for each distance were used to show the incidence rate (fig. 4A).

Expected percentages of 20.0 and 0.5 infected plants resulted from current seasons' inoculations grown between rows of diseased plants and six rows distant from diseased plants, respectively. Fair agreement of observed and calculated percentages is seen.

Incidence of potato leaf roll was shown by Gardner and Kendrick (1924) to be very variable. Wide variations were found in the percentages of current seasons infections between years and varieties although the results show decreased disease infections with increasing distance from a source of contami-

nation. A tabular arrangement of the given data is used to present the results (table 1).

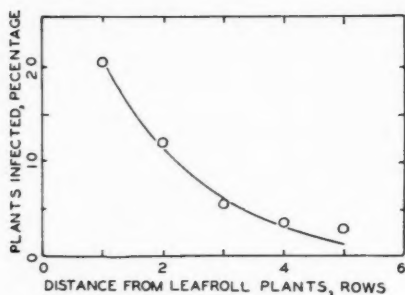


FIG. 4A.—Incidence of potato leaf roll disease (data from Murphy and Worthley).

TABLE 1.—Percentages of potato leaf roll infections at distances from known sources of the inoculum (Data from Gardner and Kendrick)

Variety	Year	Distance, feet					
		3	6	9	12	75	150
Unknown	1921	6	5	3	1
Rural	1923	78	50	3
Ohio	1923	79	32	0
Cobbler	1923	66	0	0

Definite rates of reduction of leaf roll infected plants with increasing distance are seen. Adjoining and near rows contained more diseased plants than more distant rows. Distances of 12 to 75 feet, however, gave great reductions of diseased plants, depending on the year and variety under observation.

Simpson (1938) reported on leaf roll incidence expressed by current seasons' inoculations. Through correspondence with Dr. Simpson further

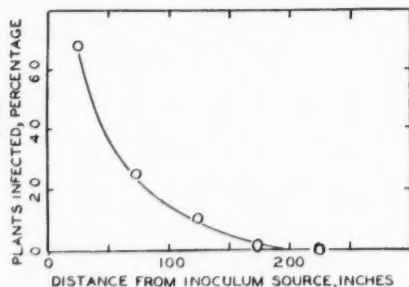


FIG. 4B.—Incidence of potato leaf roll disease (data from Simpson).

information was obtained on distances, in inches, as follows: between rows 34, between seed pieces 12, and between each four seed pieces at least 20. These distances were reported to vary somewhat but to be fair averages. By means of these data a smoothed curve was drawn to show the incidence rate (fig. 4B).

All infected plants were within 200 inches of the inoculum source. A restricted incidence is shown by these data for one season's exposure to inoculation, notwithstanding the manner in which the potato plants grow as they contact one another and intertwine between and within rows.

In a statistical study of the distribution of citrus psorosis infected trees Bitancourt and Fawcett (1944) gave data on incidence of diseased trees about an origin. Distances were given in terms of tree spaces. By means of these

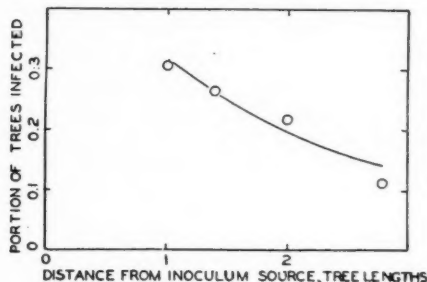


FIG. 4C.—Incidence of citrus psorosis disease (data from Bitancourt and Fawcett).

distance figures and the means of diseased trees in each, the incidence rate is presented (fig. 4C).

Distances of 2.8 tree lengths reduced the number of infected trees by more than one half. The terminal incidence of diseased trees, however, is at some more remote and unknown distance than the maximum reported observation, 2.8 tree lengths, regardless of root graft, insect vector or other method of inoculum transmission.

Kingdom Plantae

SCHIZOMYCETES

Dispersion of bacteria, as measured by the development of bacterial colonies on fresh and on salt water media, at distances from shore, was shown by Zobell (1942). The number of bacteria on sea water and fresh water nutrient agar decreased and increased, respectively, as the distance landward and seaward increased from the sea-wall. The rates of increase and decrease are illustrated (fig. 5A).

Distances of 200 feet cover the most rapid rates of change. The number of bacterial colonies approached a constant and remained practically so on fresh water medium after about 200 feet. Bacterial colonies on sea water medium, however, decreased rather constantly to 1600 meters, the most extreme distance given, and approached zero colonies at some more remote and unknown distance.

Bacterial colonies at distances from land, on the other hand, showed slight increases in number regardless of whether sea water or fresh water media were used. More colonies, however, were found on a salt water medium (fig. 5B).

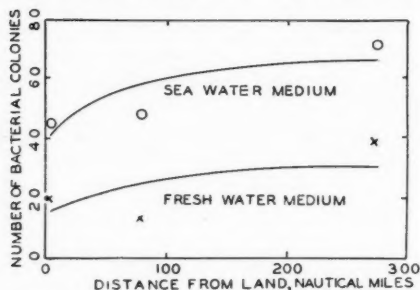
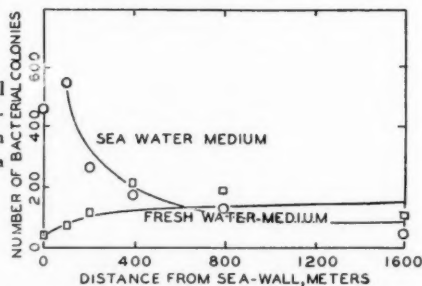


FIG. 5A.—Incidence of bacterial colonies on each of two different media at distances from land, over salt water (data from Zobell).

Similar and slight increases were found in bacterial counts with either medium used, is the most important feature of these data. More confidence would be received for these data were the regression lines in closer agreement with the observed values. Multiple sources of bacteria may account for the increases in the number of colonies with distance increase.

FIG. 5B.—Incidence of bacterial colonies on each of two different media at distances from salt water over land (data from Zobell).



Pseudomonadaceae.—Dispersion of bacterial wilt, *Phytophthora solanacearum* (EFS), Bergey et al., was shown by Metzger and Binkley (1940) to occur in potato fields. An objective of the experiment was to show that dispersion occurred rather than to show the degree of spread. It is not surprising, therefore, that in regression computations a very slight increase in the number of Gram-positive plants with an increase in distance resulted. Possibly the comparatively short distance ranges covered may account for this increase.

Dispersion of *Pseudomonas malvacearum* EFS, the organism responsible for black-arm disease of cotton, was related to rainfall as an agent of dispersion by Andrews (1936). Although the distance relationship and percentage of disease was shown by graphic representation figures were lacking for computation of a regression.

Approximations of percentages at different distances were taken from the

illustrations. These percentages are of plants affected by the disease at meters distance from the margins of old-cotton land. They are given as follows:

Distance, m.	1	2	105	175	280
Percentage	55	40	10	6	5

Whether rains or other factors were responsible the disease incidence range is seen to exist in terms of hundreds of feet. Variations which were shown by Andrews (1936) between howshas in the rates of incidence or dispersion may be expected to fluctuate somewhat because of different local conditions. This is especially true for field conditions. It is these field or natural conditions, however, which are of most value from the economic viewpoint.

FUNGI

Zobell (1942) gave data on the number of mold colonies, over ocean surfaces, as distances from land. Based on the number of mold colonies at distances from land, two curves were drawn, one for media made with sea water and the other from media made with fresh water (fig. 5C).

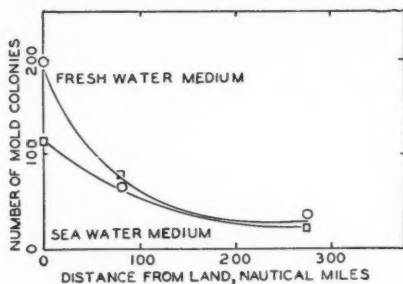


FIG. 5C.—Incidence of fungal colonies on each of two different media at distances from land, over ocean surfaces (data from Zobell).

The number of colonies decreased rather rapidly with increasing distance to near 100 nautical miles from land, then decreased with less rapidity. The curves show similar rates of decrease from near 100 to 300 miles from land with sea water and with fresh water media. Mold colonies at the 5 nautical mile distance were more numerous on fresh than on salt water media. At the 100 and 300 mile distances, however, the differences were practically nil.

PHYCOMYCETES

Peronosporaceae.—Late blight of potatoes, caused by the fungus *Phytophthora infestans* (Montagne) Debary, is a disease having considerable annual importance and causing potential epidemics with dangerous extremes. Although spores of the fungus disperse over considerable distances, perhaps in terms of miles under some conditions, the factor of greater practical value may be the rate of dispersion, or the incidence of disease as related to the source of the inoculum. Bonde and Schultz (1943) have presented data on incidence of the disease. The incidence was measured by counting the number of blight lesions per plant and also by determining the percentages of diseased plants at

distances from the apparent source of spores. Regression curves were drawn for each measure of disease incidence (fig. 5D).

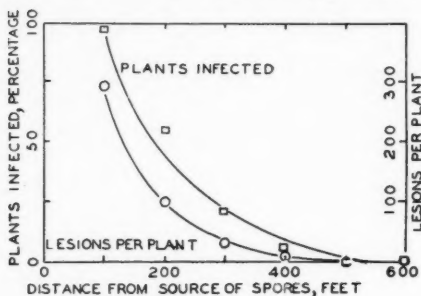


FIG. 5D.—Incidence of potato blight infections (data from Bonde and Schultz).

Both measures show similar rates of late blight incidence in which distances of 500 feet from the source show low infection frequencies. A very high infection (295.0 lesions) regresses to a low (1.7 lesions per plant) infection incidence with a difference of 400 feet distance. The prevention or eradication of primary sources of the pathogenic spores, a generally recommended control measure, is greatly emphasized by these incidence data. Further reference is made to this example under Generalizations.

Incidence data of downy mildew fungus, *Pseudoperonospora humilis* (Miy. and Tak.) Wilson, infections on hop plants were given by Magie (1942). These infections occurred at various distances from a small isolated hop yard to plants exposed for a seven-day period to dispersing fungus sporangia, and from which a curve was drawn (fig. 6A).

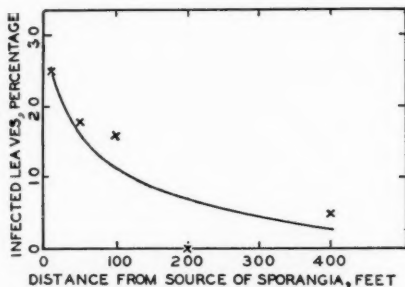


FIG. 6A.—Incidence of downy mildew fungus (data from Magie).

The regression curve shows percentages of 26.4 and 2.7 at 10 and 400 feet, respectively, indicative that nearly one-tenth as many infections may be expected at 400 as at 10 feet from the source of sporangia. Close agreement of the curve with the observed values is lacking, attributable, perhaps, to the single plants on which the observations were based.

Incidence data on the number of lesions of onion mildew, *Peronospora destructor* (Berk.) Gaspary, per 100 feet of onion row was given by Newhall

(1938). Data on vertical dispersion of mildew spores were given in terms of the numbers of cubic feet of air per spore, as part of the study. Unfortunately the vertical dispersion and incidence data are not comparable which prevents comparing vertical and horizontal dispersions. The relationship between the vertical and horizontal types is, therefore, not determined. The decrease in the number of spores at elevations above the inoculum source is discussed under the heading Vertical Dispersions given below. The regression rate of lesions on distances from the inoculum is presented (fig. 6B).

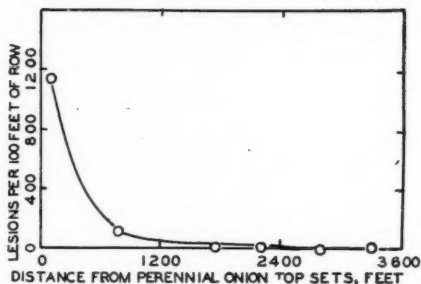


FIG. 6B.—Incidence of onion mildew disease (data from Newhall).

A rapid decline of downy mildew lesions with distance increase is shown. Most mildew was within 1,750 feet of the source. Newhall (1940) believed that, "... home plantings of perennial top sets . . . are the only sources of primary inoculum . . ." in New York State. Exclusion of plantings of top sets from in and near onion growing areas, would, therefore, be a control measure.

ASCOMYCETES

Sphaeriaceae.—Incidence of Dutch elm diseased trees, caused by *Ceratostomella ulmi* Buisman, was reported by Collins, Parker, and Dietrich (1940). Although the inoculum was probably carried by elm bark beetles in dispersion activities, as is discussed below under Scolytidae, the incidence of infected trees is presented under this heading. Midclass intervals of the distance classes and the number of diseased trees in each class are used to show the rate of incidence (fig. 6C).

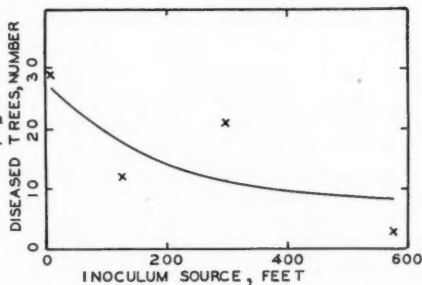


FIG. 6C.—Incidence of Dutch elm diseased trees (data from Collins et al.).

Most, 86 percent based on computed numbers, of the diseased trees were within 400 feet of the probable source of the inoculum. Close agreement of the observed and calculated values is lacking. The total incidence is at some distance more remote than 600 feet, the maximum distance under observation.

Incidence rates of the Dutch elm disease were also reported by Zentmyer et al. (1943, 1944). The number of diseased and of total elms in each radius group were transformed to percentages of trees diseased, in each of three localities. These percentages and the mid-radial distances were then transformed to probits and logarithms, respectively, for statistical analysis, by Zentmyer et al. (1944). Linear relationships were found by these transformations: an analogous similarity to dosage—response relationships. It was found that the regression formula,

$$\text{Expected probit} = 8.865 - 2.504 (\log X),$$

was common to the data in the three locations, according to Zentmyer et al. (1944). A study of the given data was made to compute a regression by the modified semi-logarithmic formula. It was found that the latter formula provided a closer alignment of calculated with observed percentages than the log-probit transformation. Chi-square tests gave 3.7 and 0.3 for the percentages from the log-probit transformations and the modified semi-logarithmic formulae, respectively, indicating the closeness of alignment. The modified semi-logarithmic formula is used, therefore, to illustrate the incidence of Dutch elm disease (fig. 6D).

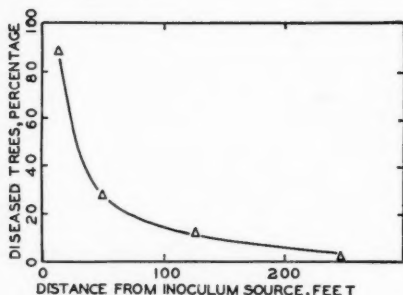


FIG. 6D.—Incidence of Dutch elm diseased trees (data from Zentmyer et al.).

A rapid rate of disease reduction is seen. At 250 feet a low percentage of diseased trees resulted. Maximum incidence, however, is at some greater distance. The rate is more rapid than that seen in figure 6C. More diseased trees were found to the north of the centers of origin of the disease organism than to the south. By relative amounts, twice as many diseased trees were found north as south of the incidence centers.

Inoculation of the diseased trees reported by Zentmyer et al. (1944) is attributed to twig crotch feeding activities of the smaller European elm bark beetle, *Scolytus multistriatus*. The frequency of inoculation of weakened, sickly, devitalized, or injured trees near beetle sources or remote from their origin is not known. Whether more or less inoculations are accomplished by crotch

feeding activities or breeding activities is also unknown. Discussion of *S. multi-striatus* dispersion is given under Scolytidae below.

Pleosporae.—The organism causing apple scab, *Venturia inaequalis* (Cke.) Wint., is known to be wind-borne. Protective sprays are applied to plants for control of the disease based on the knowledge that the spores are so dispersed. A technique of studying dispersion of apple scab ascospores was employed by Keitt et al. (1937). (1941) by which eradicant fungicide sprays were used. Scab lesions were counted in treated orchards in relation to distances from an extraneous source of ascosporic inoculum, untreated orchards.

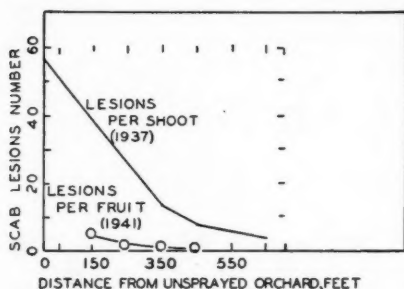


FIG. 6E.—Incidence of apple scab infections from unsprayed orchard [from Keitt et al. (1937) by a tracing reproduction, and from Keitt et al. (1941) by a curve determined from data].

Two incidence rates of apple scab are available from the reports by Keitt et al. (1937) (1941). The (1937) report was presented graphically, a tracing of which is presented herewith (fig. 6E). The (1941) report rate is given in a tabular form, the data of which were used to determine an incidence curve. The percentage portions of both reports are omitted for this presentation since the average numbers of lesions appear to portray the incidence rates more clearly.

The incidence rates shown (fig. 6E) are not considered as dissimilar as they may appear. The (1941) data were multiplied 10-fold for plotting curve studies. In this way the incidence rates of the two curves were observed to have essentially the same curvilinearity. Distances of 450 feet from the unsprayed orchards showed great reductions in apple scab infections resulting from ascosporic inoculum.

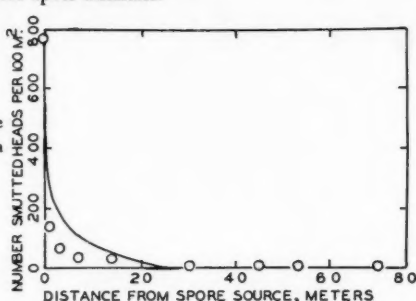
BASIDIOMYCETES

Ustilaginaceae.—An extensive study of spore dispersion manifestations of loose smut of wheat, *Ustilago tritici* Pers., was reported by Öort (1940). Loose smut was reported to spread to 100 meters distance, although it was shown that most spores terminated dispersion at much shorter distances. The given data were reduced to averages in order to illustrate the rate of spore reduction with distance increase (fig. 7A).

The data show an extremely rapid rate of decrease to between 10 and 20 meters from the spore source, followed by low levels of smut infections to 70 meters. More spore dispersion occurred in the southeast direction; least in the northwest. It was believed that hard winds caused heavier and more uniform

dispersion of spores than weak winds. Weak winds with some vertical air currents were believed to cause more variable dispersions, "... so that smut islands and more or less smut-free spots alternate."

FIG. 7A.—Incidence of loose smut of wheat (data from Öort).



Expected numbers for the regression curve were computed by the modified semi-logarithmic formula which appears to be most satisfactory with many or most dispersion or incidence data. With Öort's (1940) data, however, the log-log formula,

$$\text{Log of expected number} = 2.2619 - 0.9519 (\log X)$$

gave expected numbers which aligned more closely with the observed numbers.

Three papers give data on dispersion of the chestnut blight fungus, *Endothia parasitica* (Murr.) A. & A. A common method used in the study of this economic parasite reported by the authors was that of using sterile media in petri-dishes exposed at distances from dehiscing perithecia to catch any wind-borne spores. These examples will be discussed further in Part II. The papers by Anderson and Babcock (1912) and Rankin (1914) measured dispersion at short distances from the source, 1 inch to 50 feet and 3 inches up to 50 feet by the authors, respectively. The distance range based on the data by Heald et al. (1915) was greater, 27 to 414 feet.

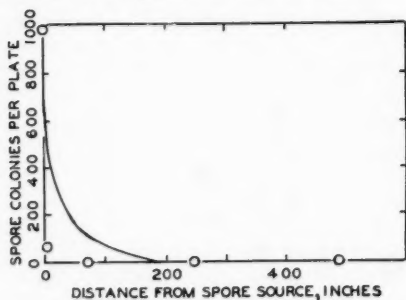


FIG. 7B.—Dispersion of chestnut blight fungus spores (data from Anderson and Babcock).

Mid-points in the distance classes given by Anderson and Babcock (1912) with their respective average number of *Endothia parasitica* colonies per plate per minute of exposure were used to determine the curve rate of dispersion

(fig. 7B). An extremely rapid rate of reduction is shown. Somewhere between 4 and 72 inches from the source a low frequency in the number of fungus colonies was reached. The number of colonies at more remote distances remained small by observed values. The spores were reported caught "downwind" from the source.

The semi-logarithmic formula was used although the log-log formula,

$$\text{Log of expected colonies} = 2.6987 - 1.3204 (\log X)$$

gave closer alignment of computed and expected values.

The dispersion data given by Heald et al. (1915) are in terms of number of ascospores per square foot of area, per minute, falling at distances ranging from 27 to 414 feet from the source, in the direction the wind was blowing. Graphic results are shown in figure 7C.

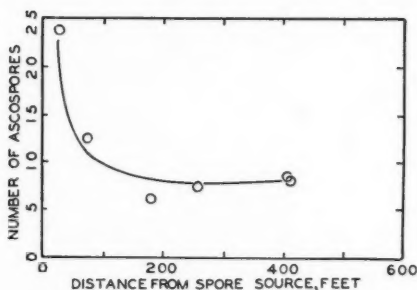


FIG. 7C.—Dispersion of chestnut blight fungus spores (data from Heald et al.).

Over three-fold more spores were caught, based on calculated numbers, at 27 than at 414 feet. Close agreement of observed and calculated values is lacking. The dispersion rate is more reduced than that computed from data given by Rankin (1914), and yet more reduced than that from the data given by Anderson and Babcock (1912).

Unidirectional dispersions are inferred from these studies in which spores are scattered by air currents. Dispersion of spores depending on air currents would appear to be susceptible to several sources of variations. Possibly one or more of these factors was operative in causing part of the variations in these observations.

The data presented by Rankin (1914) on dispersion of *Endothia parasitica*, except the 50 foot distance which was zero, given in terms of colonies per five minutes exposure, were used for determination of a regression curve (fig. 7D). Calculated numbers of colonies at 3 inches and at 15 feet were 2.09 and 0.42, respectively, five-fold greater at the shortest distance. The rate of dispersion is much more reduced than that computed from data given by Anderson and Babcock (1912).

Tilletiaceae.—Dispersion of *Tilletia* and *Bovista* spores was studied rather extensively by Stepanov (1935). Attention was given to the fall of spores at different distances and to the fall in different directions. Wind currents, the dispersion agent, carried more spores in the windward directions, and fewer

spores tangentially to the wind direction. In efforts to show the regularity of spore fall a formula was suggested to Stepanov by Professor Pomorskov. The formula is

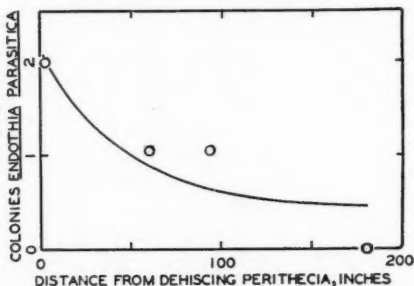
$$x = c + \frac{a}{s \cdot y}$$

in which x and y are distance and number of spores, respectively, c and a are constants calculable from experimental conditions, and s is the area occupied. The formula suggested to Stepanov uses distance but once, and that without any transformation. The use of distance twice, as in the formula,

$$\text{Expected numbers} = a + b (\log X) + c (1/x),$$

in connection with the logarithmic transformation, is considered more fundamental by Wadley and Wolfenbarger (1944).

FIG. 7D.—Dispersion of chestnut blight fungus spores (data from Rankin).



The modified semi-logarithmic formula was used to compute figures for the regression curves from the data by Stepanov (1935). The curves agree fairly well with the observed values. The data given were placed in three groups, high, intermediate, and low numbers of spores caught. The high groups were in the wind direction pathway, the intermediate group slightly, and the low group more tangential to the wind direction. The results of plotting the curves for *Tilletia* are given in figure 8A.

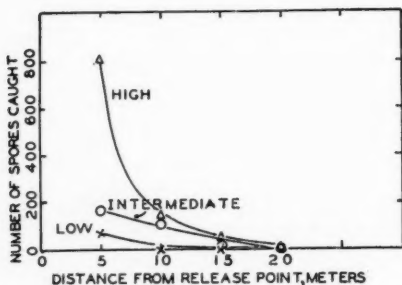


FIG. 8A.—Dispersion of *Tilletia* spores (data from Stepanov).

Distances of 20 meters from the release point showed low recoveries in directions tangential to the wind. Most spores were caught, as might be expected, in the pathway of the wind. The curves representing such dispersions appear to be more nearly segments covering but a portion of the real dispersion range. The curves in which there were but few initial spore recoveries, however, are more nearly sufficient to show the total dispersion range, since they come near to or strike the zero line nearer the origin.

Lycoperdaceae.—Recoveries of *Bovista plumbea* spores, released by Stepanov (1935) were made at distances from the liberation point. The given data were placed in groups having few, intermediate, and many spores (fig. 8B).

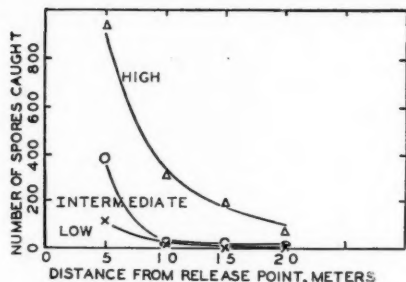


FIG. 8B.—Dispersion of *Bovista* spores (data from Stepanov).

A rapid rate of dispersion is seen in the curve from the many spore group, and a less rapid rate in the intermediate spore group. A tendency is noted for the curves with the many spore groups to have more distant dispersion than the low spore groups but they disperse correspondingly less than do the groups having few spores. A distance of 20 meters from the release point provided low numbers of spores caught regardless of the initial number.

Pucciniaceae.—Apple leaves infected by rust of cedar and apple *Gymnosporangium juniperi-virginiana* Schw., were found by Jones and Bartholomew (1915) and Reed and Crabill (1915) to decrease at distances from the apparent source of inoculum.

In the computation of the regression from the data from Jones and Bartholomew (1915) a distance of zero was used for, "at base of Cedar Bluffs" and the mile units were changed to rods (fig. 8C). The percentage of infected leaves at one mile indicates that dispersion terminated at some more remote and unknown distance. Individual observations at given distances show much uniformity but collective observations over the distance range lack agreement with the computed values.

Cedar apple rust spots on apple leaves were found by Reed and Crabill (1915) to decrease with distance increase over the distance range of 50 to 300 meters from cedars. The meter units were converted to rod units for calculation of the incidence curve (fig. 8C).

Computed leaf infections were nearly 12 per cent as high at 300 as at 50 meters. The two incidence curves have similar rates of slope. As a result they

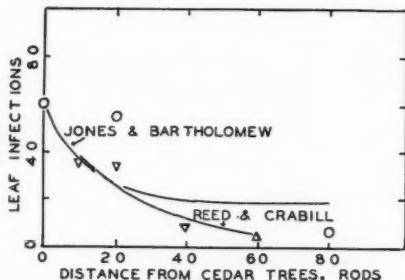
are both more reliable in indicating the distance range and rate of infection with distance increase that may be expected for cedar and apple rust.

The curves shown were computed by the modified semi-logarithmic formula. Closer alignment of observed and computed values, however, was apparently obtained by the use of the straight-line formula,

$$\text{Expected number} = a + b(X).$$

Dispersion studies of cereal or stem rust, *Puccinia graminis* Pers., spores by Stakman and his co-workers (1923) (1939) have shown that showers of spores occur throughout the vast Missouri-Mississippi river drainage system, the great wheat producing region of the United States.

FIG. 8C.—Incidence of apple leaf infections from cedar and apple rust (data from Jones and Bartholomew and from Reed and Crabill).



In some early work over a comparatively short distance range (short, evidently for *Puccinia graminis*) catches of spores "over" barberry bushes and at distances up to 25 miles from barberry bushes were reported by Stakman et al. (1923). A smoothed curve was drawn from these using aecio- and urediniospores (fig. 8D).

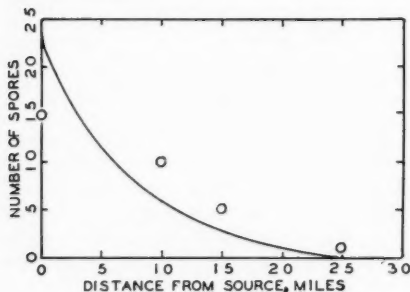


FIG. 8D.—Dispersion of aecio- and urediniospores of wheat stem rust [data from Stakman et al. (1923)].

Almost one-twentyfifth of the total expected number of spores was caught at "25 miles from," as "over" the barberry bushes. The data from this early work were undoubtedly of much value in later studies since they gave some indication of the distance range that might be expected from more extensive experiments.

Stakman and Hamilton (1939) reported on the number of spores caught at cities ranging from Dallas, Texas, to Madison, Wisconsin. Map distances were computed from Dallas, Texas, to each of the cities where the trapping stations caught the spores. With Dallas as the assumed origin and the average number of spores caught at each trap, per square foot, for the two-day records, May 25 and 26, a curve was drawn (fig. 9A).

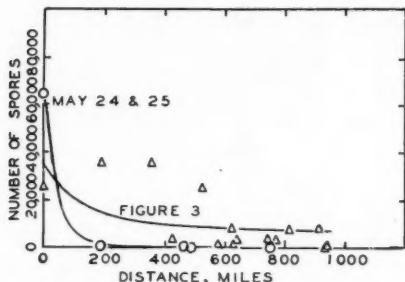


FIG. 9A.—Dispersion of wheat stem rust spores [data from Stakman and Hamilton (1939)].

Rapid decreases in the number of spores caught is indicated to distances of about 200 miles, followed by slight decreases to 750 miles. Agreement of observed and calculated values is fair.

Additional dispersion data were taken on cereal rust spores from the report by Stakman and Hamilton (1939, fig. 3) from which another curve was drawn (fig. 9A). This curve is similar to that given for May 24 and 25 data in the curvature of its terminal portion. It is dissimilar, however, to the May 24 and 25 curve in its initial portion. Expected numbers of spores at the assumed origin and 940 miles are 34,035 and 6,975 per square foot, respectively. Lack of agreement between observed and calculated values and the noted dissimilarity may induce inquiry of the fidelity of this curve to illustrate the usual rate of *Puccinia graminis* dispersion of urediniospores.

Melampsoraceae.—A total of four records was located with dispersion or incidence data on the white pine blister rust, *Cronartium ribicola* F. von Wald. Different locations and different conditions are represented in these reports. They are similar, however, in that all are field data and are given in percentages of infected trees at different distances from the apparent source of the inoculum, plants of the *Ribes* spp., obligate hosts of *C. ribicola*.

Data collected by the Division of Plant Disease Control of the United States Bureau of Entomology and Plant Quarantine, (1938), indicated the number of infected trees at distances from a stream, the usual habitat of *Ribes* plants. The distance range was 0 to 22½ chains (up to 1485 feet). A curve was drawn from the given data (fig. 9B).

A rapid initial rate of decrease followed by a continuously decelerating rate indicates that a low incidence of disease infections was reached at 22½ chains from a stream. Total incidence, however, was reached at some more remote and unknown distance. There is close agreement of computed with observed values.

Incidence of white pine blister rust infected trees around black currant bushes was reported by Posey and Ford (1924). The data which were given by directional quadrants were analyzed statistically to determine differences attributable to directional influences. Most infected trees were in the south,

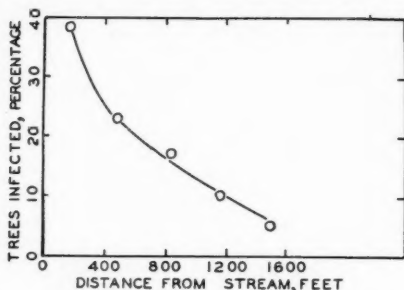
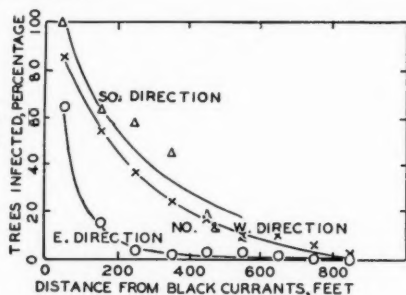


FIG. 9B.—Incidence of white pine blister rust infected trees (data from U. S. Bureau of Entomology and Plant Quarantine).

fewer were in the east. The data from the west and north were so similar that they were justifiably combined. Three curves were, therefore, drawn for these incidence data (fig. 9C).

Remarkably similar rates of regression are seen for the southern and the combined west and north directions. The eastern curve showed considerably fewer infections. Low levels of infections are indicated at distances of 800 to 900 feet regardless of directional influences.

FIG. 9C.—Incidence of white pine blister rust infected trees (data from Posey and Ford).



In showing the unimportance of cultivated red currants with reference to white pine blister rust Snell (1941) gave data on blister rust infections centered around the, "... two largest wild gooseberry bushes." This infection-distance relationship is illustrated in figure 9D.

About one-third as many infections occurred at 650 as at 50 feet. The incidence rate is seen similar to those computed from data given by Posey and Ford (1924) shown in figure 9C. The observed infection, 26 per cent, between 500 and 600 feet from the gooseberry bushes was reportedly near cultivated red currants. Rust infections are shown to be related, therefore, to the presence of gooseberry bushes.

Decreases in blister rust infections as distances increased from two *Ribes*

species, *R. lacustre* (Pers.) Poir. and *R. viscosissimum* Pursh., were shown by Buchanan and Kimmey (1938). A curve was determined for each *Ribes* species although no especial significance is attached to the species factor. Since different sized trees have unequal frequencies of infections (large trees are more likely to become infected than small ones since they are larger targets for the inoculum to strike) the data for the curves were taken from records in which the average size of the trees was five feet (fig. 10A).

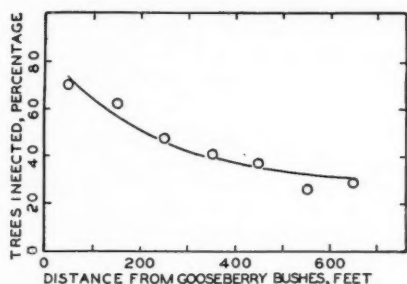
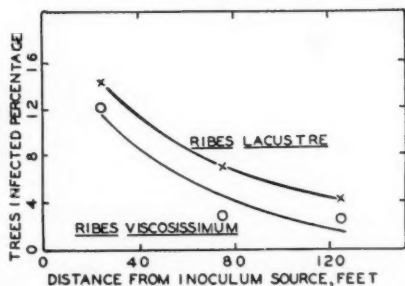


FIG. 9D.—Incidence of white pine blister rust infected trees (data from Snell).

Between 11 and 12 per cent reductions are shown over the 100 foot distance range. Similar curvilinearities of the curves add confidence one to the other. No difference in the dispersion rate is seen which might be attributable to *Ribes* species.

FIG. 10A.—Incidence of white pine blister rust infected trees (data from Buchanan and Kimmey).



Studies of the regression curves of white pine blister rust infections indicate two rates of infection incidences and these may be termed more rapid and less rapid incidence rates. The more rapid incidence rates are shown by the data from Buchanan and Kimmey, and Posey and Ford, figures 10A and 9C. The more reduced incidence rates are exemplified by the data from the Division of Plant Disease Control and from Snell, figures 9B and 9D. The data presented in the first two mentioned papers may have been taken close to the inoculum, whereas the data from the Division of Plant Disease Control, as indicated above, were taken in relation to the distance from a stream. Snell's data were taken in zones whose origin centered at the, "... two largest goose-

berry bushes." It seems likely, therefore, that for the last two mentioned papers there may have been other sources of sporidia than the assumed origin, with the result that the curves assumed a more gentle slope.

Polyporaceae.—A study in the pinetum at Michigan State College by Strong (1941) revealed that the velvet-topped fungus, *Polyporus schweinitzii* Fr., dispersed from an infected tree to adjacent trees over a four-year period throughout the plantation. Tree distances were computed by triangulation, and the percentage of fallen trees was determined for each distance class. A curve was prepared to show the incidence of the disease (fig. 10B).

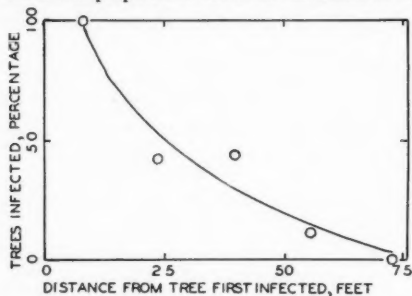


FIG. 10B.—Incidence of velvet-topped fungus infections (data from Strong).

A quotation from the author that, "... the four trees most extensively rotted were nearest to the location of the tree first affected," emphasizes the importance of proximity to the source of the inoculum. The expected percentages of affected trees are 98.2, 52.3, 31.0, and 16.9 at the midclass distances of 8, 24, 40, and 56 feet, respectively, to show the degree of incidence. The maximum dispersion distance is at some distance more remote than 56 feet.

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Pinaceae.—Disseminules from this family may be one or more of three types, seed, pollen or seedlings. Some quantitative data are available on pollen and seed dispersion although considerable is known from the qualitative aspect. The general work on pollen analysis by Erdtman (1943) is also valuable.

Pollen grain counts per square millimeter of area on lightships at two distances from land were given by Hesselman (1919). These are given as follows:

Pollen kind	Distance from land (km.)	
	30	55
Pine	2,390	1,069
Spruce	6,961	4,089

Wide spread pollen dispersion is indicated. Pollen of Pinaceae appears to be dispersed upwards to 100 miles from the source.

More information was found on seed dispersion than on pollen dispersion. Seed production and dispersion are factors of practical importance in reseeded or reforestation in a conservation program. Most of the references to seed dispersion give the number of seedlings per acre unit. It is of interest to know the number of seedlings recommended per acre. Distances of 6 x 6 or 6 x 8 feet between trees are the general recommendations for planting trees. In terms of the number per acre the numbers are 1210 or 908. It would appear that natural stocking with less than this number, except as recommended for different soil types, mixed stands, or some other reason, would be insufficient.

The question of how far are seeds dispersed cannot be definitely answered any more than for other organisms. A sound philosophy from a practical viewpoint has been expressed in regard to the natural establishment of pine. According to McQuilken (1940) it is, "... not unusual to find seedlings one-fourth or more miles from seed trees, the pertinent question is the distance to which seeds are dispersed in sufficient numbers to produce a satisfactory density of stocking."

Considerable data on a number of tree species were given in the paper by Hofmann (1911). Some seeds remained unharmed, sprouted, and became seedlings after fire had burned over them. In tables 2 and 3 the percentages of seedlings were given for year classes, as 0-5, 6-10, and over 10, depending on the length of time after burning before the number of seedlings was counted. The interpretation given here is that the 0-5 year classes were used, since the author reported that, "... the occurrence of the age class 0 to 5 years is limited to the vicinity of seed trees or to localities ... within the influence of these trees."

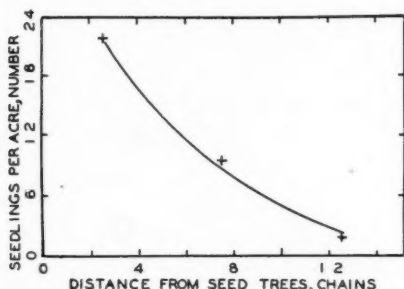


FIG. 11A.—Incidence of silver fir seedlings (data from Hofmann).

Data on incidence of silver fir, *Abies alba* Mills, seedlings per acre were given by Hofmann (1911). The rate of reseeded after a burn at distances from seed trees for periods of years was given. Midclass points of the distance intervals were determined, and 12.5 chains was used for the distance class of "over 10." The data from the time period of 0 to 5 years were used to show the incidence of silver fir stocking (fig. 11A).

Plants resulting from natural seedings are rapidly reduced in numbers as the distances from the seed trees are increased. The expected and the observed values agree well. Expected numbers of seedlings per acre were 21.9, 8.9 and 2.9 at midclass distances of 2.5, 7.5, and 12.5 chains, respectively.

Seedlings of noble fir, *Abies nobilis* Lindl., were counted by Hofmann (1911) at each of three locations, at distances from the apparent seed source. The data from two locations were combined to compute data for a single curve since statistical analyses showed insignificant differences between them. Two curves, therefore, were drawn (fig. 11B).

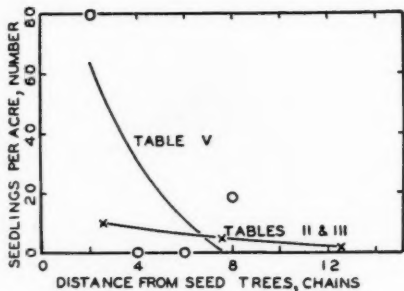


FIG. 11B.—Incidence of noble fir seedlings (data from Hofmann).

The two curves indicative of noble fir seeding differ considerably in slope. Fair alignment of the observed values and the smoothed curve is seen in the data from tables 2 and 3, but they differ considerably in the data from table 5. In table 5 observed values of 80, 0, 0, and 20 seedlings per acre at distances of 2, 4, 6, and 8 chains, respectively, from seed trees were reported. These data suggest that some multiple of 20 was employed in sampling, and that additional samples might give observed values deserving more recognition.

Incidence of natural stocking of Douglas-fir, *Pseudotsuga taxifolia* (Lam.) Butler, on burned-over land at distances from the probable seed source was given by Hofmann (1911). Data from two locations were combined for a single incidence curve while data from a third location were used to show a second incidence curve (fig. 11C).

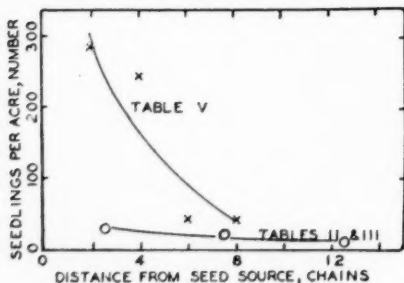
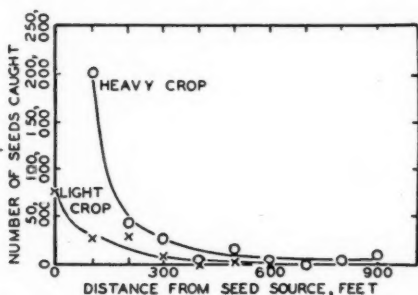


FIG. 11C.—Incidence of natural stocking of Douglas-fir (data from Hofmann).

The effectiveness of natural seeding to distances greater than two chains was considered inadequate to give a satisfactory stand. Dependence on natural stocking of Douglas-fir from seed source trees appears to be a restricted or a slow process of reforestation.

In studying seed dispersion Isaac (1930) gave data on seed fall of the Douglas-fir at distances from the source, covering a two year period. The abundant seed fall one year was called a "heavy crop," and the lighter seed fall the ensuing year was called a "light crop." A curve was drawn for each crop (fig. 11D).

FIG. 11D.—Dispersion of Douglas-fir seed (data from Isaac).



Rapid rates of regression to distances near 200 feet from the seed source are observed. A very striking feature of these curves is the tendency for their intersection at near 700 feet from the source. See also the discussion of this example in Part 2.

Hofmann (1911) presented data on incidence of western hemlock, *Tsuga heterophylla* (Rof.) Sarg., seedlings at distances from seed trees. Taken at four locations these data were given in four distance ranges, except those in tables 2 and 3 which were combined for a single curve. Three curves, therefore, were drawn (fig. 12A).

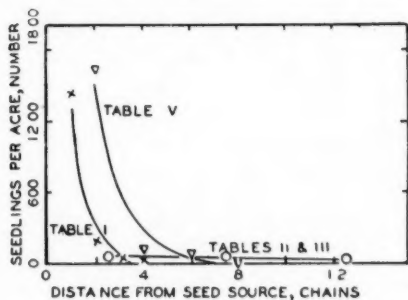


FIG. 12A.—Natural stocking of western hemlock (data from Hofmann).

The curves from the data in tables 1 and 5 with similar contours indicate a limited seed dispersion of western hemlock. Distances greater than four

chains had few seedlings. The curve combined from the data in tables 2 and 3 had but a slight declination, which is probably attributable, in part at least, to seed dispersions previous to the burn.

Black spruce seed, *Picea mariana* (Mill) B. S. S., was reported by the Lake States Forest Experiment Station (1939) to have limited dispersion. Traps were placed at various distances from the edge of a stand of seed trees, in line with the prevailing wind, over a two year period, to catch the seed. A curve was drawn from these data (fig. 13B).

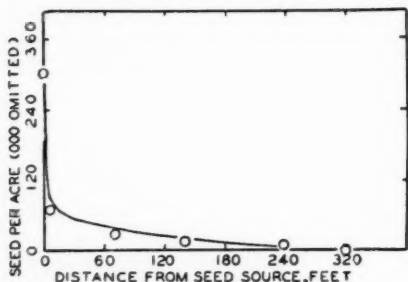


FIG. 12B.—Dispersion of black spruce seed (data from Lake States Forest Experiment Station).

A very rapid falling off in the amount of seed caught with increase in distance to five feet is shown. A reduced dispersion rate is indicated from 5 to over 200 feet from the seed source.

Pine stand stocking in fields abandoned 1 to 3 and 4 to 12 years was reported by McQuilken (1940). The data given by this author are presented in a slightly different manner from most dispersion or incidence data. The average distance from the seed source is given at which 500, 1,000, and 2,000 seedlings per acre were found. Two curves were drawn, one for each time—abandonment group (fig. 12C).

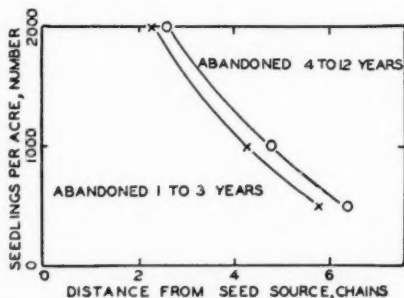


FIG. 12C.—Pine stand stocking (data from McQuilken).

Very close agreement between observed and calculated values is shown. Fields abandoned 1 to 3 years were stocked with 900 or more seedlings per acre up to near $4\frac{1}{2}$ chains from the seed source. In fields abandoned 4 to 12 years the stocking of seedlings of 900 or more extended to 5 chains from the

seed source. Slightly different curves having slightly different slopes are shown. See also the discussion in Part II.

Western white pine, *Pinus monticola* Dougl., seedlings were shown by Hofmann (1911) to grow restrictedly near the seed source. Since seedlings are the outcome of seed dispersion the seeds apparently have a limited dispersion from source trees of this important forest species (fig. 12D).

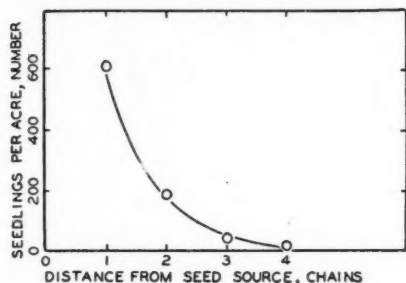
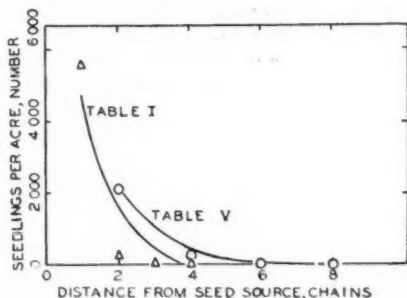


FIG. 12D.—Incidence of western white pine seedlings (data from Hofmann).

A rapid rate of regression at near two chains distance followed by a reduced terminal rate is shown. The natural seeding at distances greater than about two chains is insufficient to meet the desired forest stocking.

Western red cedar, *Juniperus scopularum* Sarg., seed dispersion as measured by seedlings per acre, was given by Hofmann (1911). From a practical viewpoint the incidence of redcedar seeding appears limited to very short distances. Seeding incidence of this species is indicated to be shorter than for other species of the Pinaceae. Two curves were drawn (fig. 13A).

FIG. 13A.—Incidence of western red-cedar seedlings (data from Hofmann).



Distances of more than three chains show greatly reduced numbers of seedlings per acre. Both regressions illustrate rapid rates of reduction to low levels of seedling incidence.

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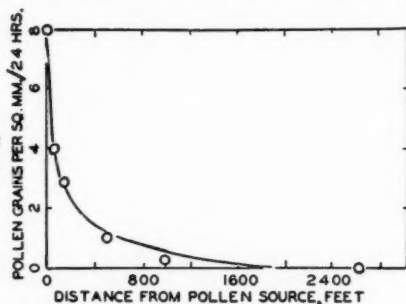
An important factor in certain plant breeding work is the distance and amount of pollen dispersion that may affect varieties, strains, yields or other

reactions which it is desired to control. Not only pollen but also seeds and plants of this class may be dispersed. It is observed, however, that the reviews under this heading all pertain to the dispersion of pollen.

Juglandaceae.—Data were given by Crane, Reed, and Wood (1937) on the dispersion of walnut pollen, *Juglans regis* L., pollen shedding at its highest, per square millimeter, per 24 hour period. The dispersion rate is shown in figure 14A.

Most of the pollen fell within a few hundred feet of the source. Nearly

FIG. 14A.—Dispersion of walnut pollen (data from Crane et al.).



one-eighth as many grains fell at 500 feet from the source trees as under them. Agreement of the observed and calculated values is quite close, indicative of a satisfactory sampling procedure. Zero pollen fall was computed to have been reached at near 1600 feet from the source trees.

Vitaceae.—Muscardine grapes, *Vitis rotundifolia* Michx., were shown by Armstrong (1936) to produce more fruit nearer staminate or male vines than on vines more distant from them. These grapes are largely self-sterile although some vines have blossoms of both sexes. The presence of nearby staminate vines, however, provided increased yields. The distances were reported in terms of rows which were used in drawing the regression curve (fig. 14B).

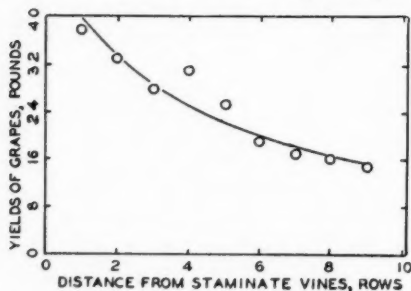


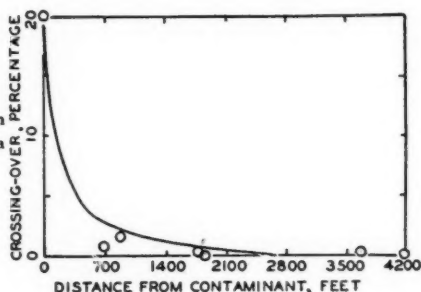
FIG. 14B.—Incidence of frape yields (data from Armstrong).

The author stated, "... past the 4th row, about 50 feet, from the males the yields drop off." Expected yields of 40.7 and 25 pounds per vine in the 1st and 4th rows, respectively, show the amounts of reduction between these near

rows. The expected poundage of the 10th row is 14.5. Agreement of the observed values with the smoothed curve is fair.

Malvaceae.—Dispersion of cotton pollen, *Gossypium hirsutum* L., was studied by Brown (1938) and by Pope et al. (1944) as determined by cross-breeding tests. Crossing of red- on green-plant cotton strains, whether wind, insects, or other agents are distributors of the pollen, under field conditions extends over a period of time and offers a very satisfactory method of testing dispersion.

FIG. 14C.—Incidence of red- on green-plant cotton strains (data from Pope et al.).



Barriers of corn plants were used to protect unlike cotton strains, as reported by Pope et al. (1944). Distances in terms of feet from 0 to 4,200, and barrier distances of 0, 3, 6, and 9 corn rows (whatever distance units as feet, meters, or other measurement units separated the rows is not known) were given. Two curves were drawn; the feet-distance data are given in figure 14C, and the row-distance data in figure 14D.

A very small amount (0.02 per cent) of crossing was observed at 4,200 feet, the smoothed curve, however, reaches zero at near 2,000 feet. Reduced cross-pollination by more than one-half is shown by the combined influences of the corn plants and the 9-row distance. Distance effects, unimpeded by corn row barriers, were shown by natural crossing to be operative for several hundreds of feet.

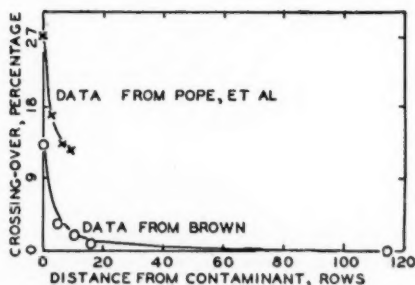


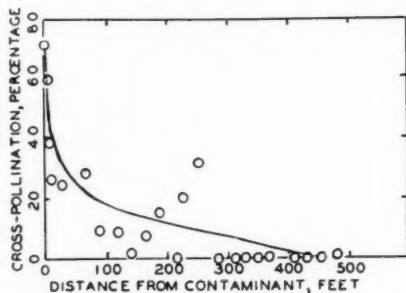
FIG. 14D.—Incidence of red- on green-plant cotton strains (data from Pope et al.) and from Brown).

Red-leaf on green-leaf cotton crossing was reported by Brown to occur at distances as much as 114 rows away. A smoothed curve was drawn from the percentages of crossing and row distances given (fig. 14D).

Fair agreement of the observed points with the curve exists, except at the 114th row. The curve, however, reaches zero at near the hundredth row. It was observed by Brown (1938) that more crossing was found one year than another. It was attributed to a larger amount of contaminant pollen at the source.

Cruciferae.—Natural cross-pollination of the radish, *Raphanus sativus* L., a self-incompatible crop plant which must receive pollen from another plant to produce seed, was studied by Crane and Mather (1943). Characteristic root colors of different strains permitted measurements of crossing at distances from a known source (fig. 15A).

FIG. 15A.—Incidence of cross-pollination of the radish (data from Crane and Mather).



A rapid rate of reduction is seen up to about 10 feet from the source, followed by less rapid falling off in crossing. Zero crossing was reached at near 420 feet, as determined by the smoothed curve.

Rosaceae.—In connection with apple pollination reference is made to the Apidae and the dispersion of honeybees to apple blossoms at different distances from colony location is discussed.

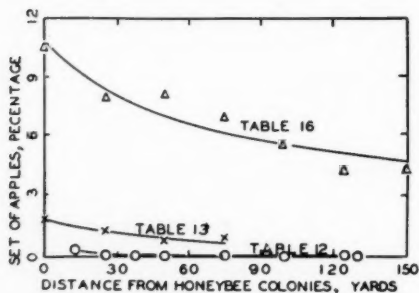


FIG. 15B.—Incidence of apple fruit set at distances from honeybee colonies (data from Hutson).

Results of pollen dispersion, as measured in terms of apple fruit set, *Malus pumila* Mill., was shown by Hutson (1926) to decrease with increase of dis-

tance from honeybee colonies. In a comparison of fruit set on the varieties Smith Cider and Winesap it was found that there was no difference attributable to varieties so that a combination of the data for a single curve was justified. The data from three different tables were used for drawing separate curves (fig. 15B).

Expected percentages of fruit set were 0.23 and 0.03 at 12.5 and 130.5 yards, respectively, over seven-fold greater at the shortest distance observed (table 12). Fruit set, by the curve, was 1.86 and 0.90 at 1 and 75 yards, respectively, which is but slightly over two-fold increase. The expected percentages of fruit set at the colonies (calculated as of zero) and 150 yards were 11.2 and 5.3, respectively, over two-fold greater at the nearest distance.

Considerable variations are known to exist in sets of fruit from year to year and in different locations. These variations are attributable to a number of factors, some of which may be, in part, controlled by man. Further efforts are needed to determine, evaluate, and develop corrective measures among these factors whenever it may be practicable.

The number of seeds in an apple may be taken as an index of the pollination conditions in an orchard. This is illustrated by an example reported by MacDaniels and Heinicke (1937) on the incidence of seed per apple in rows of McIntosh at distances from Jonathan trees. From data given in terms of tree rows and the average number of seeds per fruit a curve was determined (fig. 15C).

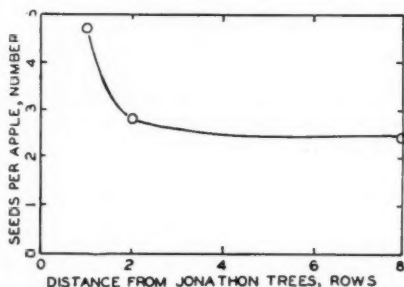


FIG. 15C.—Incidence of apple seeds per fruit at distances from Jonathan trees (data from MacDaniels and Heinicke).

The incidence of seed increase was markedly restricted to the row adjoining Jonathan trees, source of the pollen. The few fruits found in the more distant rows were often misshapen, a further symptom of incomplete pollination. Distance affected the seed incidence but little beyond the row next to the Jonathan trees.

In stressing the importance of cross pollenizers and honeybees in a peach orchard, *Prunus persica* (L.) Stokes, a report was given by Gardner and Johnston (1926). The Elberta was the cross-pollenizer, on the Hale variety. The percentages of blossoms maturing fruit at distances from the Elberta trees were the criteria of measurement. Distances were given as trees (1) "adjoining the Elberta," (2) "here and there through . . . the block" and (3) "farthest

removed from the Elberta." Units of 1, 2, and 3 were assumed for the distance relationships of these trees, and a curve was drawn (fig. 15D).

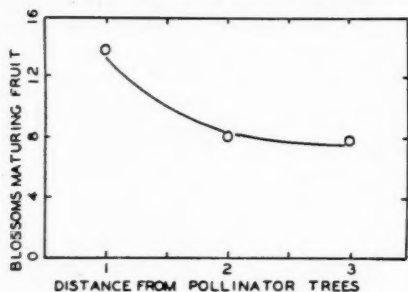


FIG. 15D.—Incidence of peach blossoms maturing fruit at distances from a cross-pollinizer (data from Gardner and Johnston).

A decrease in the percentages of blossoms maturing fruit with increase in distance from the Elberta trees is shown. Since the units of distance are unknown the assumed units may fail to present accurately the related observations. It is an example of word distance descriptions, however, which it is hoped will be replaced in future work by quantitative descriptions in commonly used unit systems.

Linaceae.—Data on natural cross-pollination of fiber-flax, *Linum angustifolium*, were given by Robinson (1937). Blue-flowering were crossed on white-flowering plants and vice versa. Data were given covering different years results and from widely separated localities. Although the author believed more crossing occurred on blue- than in white-flowering plants, and slightly less crossing occurred in Oregon than in Michigan, all figures were totalled and averaged for each given distance. A curve was drawn from these averages (fig. 16A).

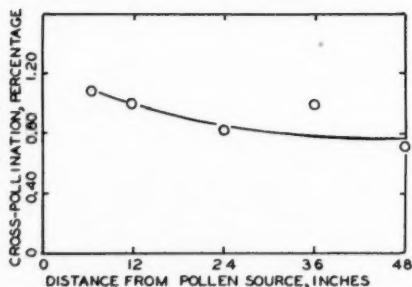


FIG. 16A.—Incidence of blue-flowering on white-flowering fiber-flax (data from Robinson).

Cross-pollination existed at 48 inches at rates slightly less than at 6 inches. Depending on the objective sought, cross-pollination of fiber flax appears to be of little practical significance in view of the small differences shown.

Leguminosae.—Megee and Kelty (1932) reported on clover seed produc-

tion at distances from honeybee colonies. Data were given covering two seasons' observations on alsike clover, *Trifolium hybridum* L. (fig. 16B).

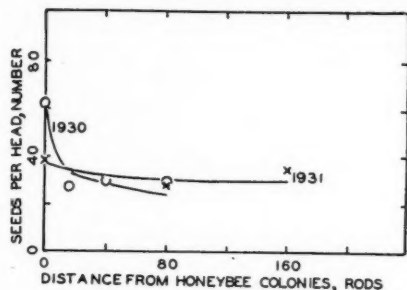


FIG. 16B.—Incidence of seeds per head of clover at distances from honeybee colonies (data from Megee and Kelty).

Wide differences between years are indicated by the different seasons' results. In the 1930 curve 59.1 and 24.2 seeds were calculated for the 0.5 and 80.0 rod distances, respectively, and for the 1931 curve the calculated number of seeds were 37.5 and 32.6 at 1 and 80 rods, respectively.

June clover seed production was almost as great at 120 as at 1 rod from honeybee colonies, according to data given by Megee and Kelty (1932) (fig. 16C).

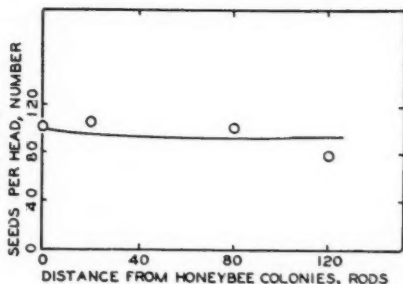


FIG. 16C.—Incidence of June clover seeds per head at distances from honeybee colonies (data from Megee and Kelty).

Seed production of June clover, based on the smoothed curve, was 100.8 and 95.7 seeds per head at 0.5 and 120.0 rods distance from honeybee colonies, respectively.

Studies of the curves in figures 16B and 16C indicate that differences in the numbers of seed per head at different distances are slight, except as indicated by the 1930 curve for alsike clover. The distances covered may be short to show wide differences. The differences between the 1930 and the 1931 curves in figure 16B and the lack of agreement in both curves suggest that additional observations are necessary for further understanding of the incidence of clover seed production at distances from honeybee colonies.

Incidence of natural crossings in lima beans, *Phaseolus lunatus*, and

of the common bean, *P. vulgaris*, both of which are usually considered to be self pollinated, is shown for each species from data given by Barrons (1938) (fig. 16D). Similar incidence rates of natural crossing are seen for lima and common beans. A higher incidence of natural crossing, however, is seen for common than for lima beans. The somewhat flattened curves at nine yards distance shows that crossing must terminate at some more remote and unknown distance.

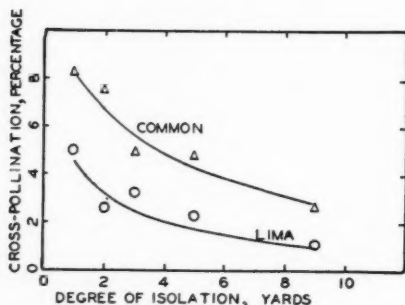


FIG. 16D.—Incidence rates of crossing of lima and common beans (data from Barrons).

Gramineae.—Dispersion of rye pollen, as manifested by cross-fertilization, was shown by Röemer (1931) to occur with slight decreases which reached a low level at about 280 centimeters. Cross-fertilization occurred at greater distances, however, in fluctuating percentages without showing a definite trend. Two curves were drawn from data referring to two directions (fig. 17A).

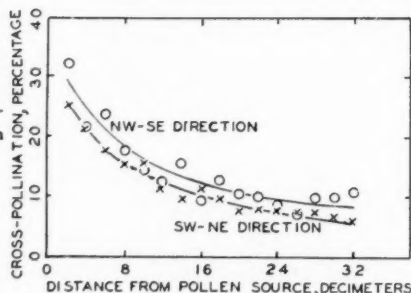


FIG. 17A.—Incidence of cross-fertilization of rye (data from Röemer).

Two nearly isoclinical curves resulted from the different directions. A higher percentage of cross-fertilization existed in the first row distance of the NW-SE directions and remained higher over the entire distance range covered. Further reference is made to this example in Part II.

Quantitative data on cross-pollination of corn, *Zea mays* L., a generally recognized occurrence between two corn varieties, were given by Haber (1935). Averages were computed for each distance class which with their mid-points were used for the drafting of a smoothed curve (fig. 17B).

According to the observed values nearly one-fourth as much contaminated corn was found at 315 feet as between 5 and 35 feet. Decreasing rates of contamination were reported up to 400 feet at which an occasional kernel was found. The curve lacks close agreement with the observed values.

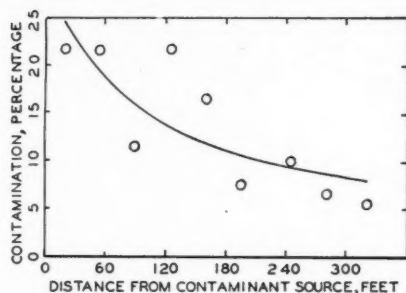


FIG. 17B.—Incidence of cross-pollination of corn (data from Haber).

Solanaceae.—Natural crossing, pollen dispersion with resultant pollination devoid of controlled factors, in tomatoes, *Lycopersicum esculentum*, was shown by Currence and Jenkins (1942) to occur in terms of feet. Conversion of percentages of cross-pollination to logarithms, according to the authors, gave a correlation coefficient of $-.846$, while the non-transformed percentages gave $-.698$, which indicates a closer correlation of percentages with distance by logarithmic transformation. No regression formula, however, was given. Although, "... certain observed means depart somewhat from the theoretical values . . .," as phrased by Currence and Jenkins (1942), they tend to an alignment about an incidence curve of cross-pollination (fig. 17C).

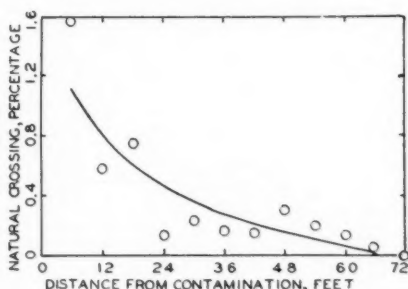


FIG. 17C.—Incidence of natural crossing of the tomato (data from Currence and Jenkins).

A low initial incidence of natural crossing is made lower by distance increases in the usually self-pollinated tomato. A distance of 50 feet was demonstrated to show great reductions in the percentage of crossing. Although an observed distance of 72 feet gave zero crossing, the smoothed curve shows that natural crossing may be expected at more remote distances.

Kingdom Animalia

INSECTA

Locustidae.—Migratory locusts may and often do disperse long distances. Some locusts hatch from the egg, develop to maturity, mate, deposit eggs, and perish near their origin, while others are known to become "migratory." The phases of locusts are discussed by Faure (1932), however, and an extensive treatise by Uvarov (1928) gives considerable information. There is much, especially from a quantitative viewpoint, that remains unknown. Only one paper was located which reported the numbers and distances to which grasshoppers dispersed.

Recoveries were made by Willis (1939) of 30 of a total of 20,440 marked and liberated grasshoppers of two species, *Dissosteira longipennis* (Thos.) and *Melanoplus mexicanus* Sauss., both of which are considered migratory. Releases were made in two different years: in Colorado in 1937, and in Montana in 1938. In order to secure as much information as possible and to encourage further dispersion studies in this group the data from the two years, species, and states were combined and used for drawing a single curve (fig. 18A).

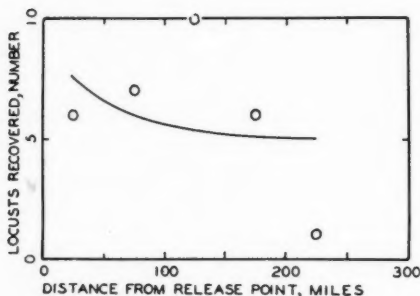


FIG. 18A.—Dispersion of migratory grasshoppers (data from Willis).

A decrease in the number of recovered insects with increase in distance is shown by these meager data. Wide variations are shown between the observed and calculated numbers. More data would be desirable, therefore, to eliminate the extremes and ensure greater reliability. The distance involved (hundreds of miles), however, is the significant feature, and may be of value for planning any further study. A unidirectional northward dispersion of grasshoppers was reported.

Cicadellidae.—In connection with studies for the control of lettuce and endive for late fall crops Linn (1940) liberated marked, six-spotted leafhoppers, *Macrostelus divisus* (Uhl.), and later recovered a small portion (0.25 per cent) of those liberated. Although a statistical test showed insignificant differences between directions, Linn indicated that more insects dispersed with the prevailing winds in an easterly direction. The data from all directions were combined for drawing a single curve (fig. 18B).

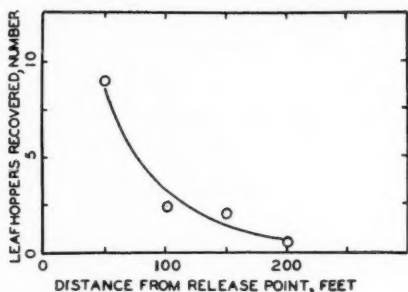


FIG. 18B.—Dispersion of the six-spotted leafhopper (data from Linn).

Most of the dispersion occurred within 200 feet of the liberation point. This radial distance was used in the development of control measures affecting localized areas, and was so reported by Linn (1940).

Linn (1940) also reported on the time required for six-spotted leafhopper, *Macrostes divisus* (Uhl.) dispersion. The curves, having positive regression, slope upward and show how more time is required to disperse greater distances (fig. 18C).

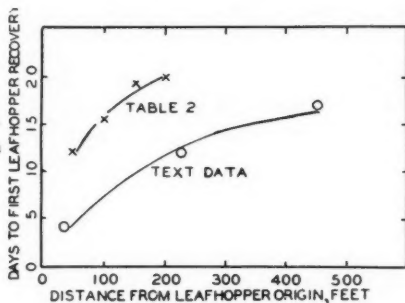


FIG. 18C.—Time required for six-spotted leafhopper dispersion (data from Linn).

Slight slopes of the curves are indicated for the comparatively few data. The two curves drawn have very similar rates of slope, which enhances their value and that of the principle involved.

For comparative purposes the distance-dispersion curve is also shown. It slopes downward. Dispersion-time is thus shown to be inversely related to dispersion-distance, and will be further discussed under Generalizations.

Representatives of 50 species of leafhoppers were taken by light traps off shore in Delaware Bay by Stearns and MacCreary (1938). A feature of these data is that the traps functioned throughout the summer months, May to September, inclusive, thus covering the entire season. Three curves were drawn from the data given, (1) total leafhoppers of all species, (2) the potato leaf-

hopper, *Empoasca fabae* (Harr.), and (3) the six-spotted leafhopper, *Macrosteles divinus* (Uhl.) (fig. 18D).

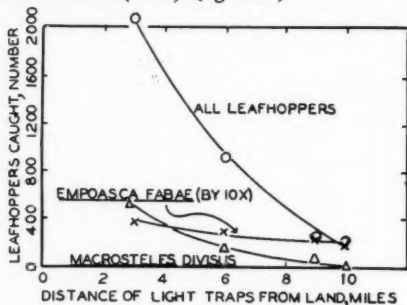


FIG. 18D.—Leafhopper dispersion (data from Stearns and MacCreary).

The curves agree well with the observed numbers. A more rapid decrease for total leafhoppers of all species is shown than for the species *Empoasca fabae* and *Macrosteles divinus*. This suggests that the more important economic species, *E. fabae* and *M. divinus*, have more widespread dispersion than many of most species generally accepted as having little economic value. Studies of these species might be considered from the viewpoint of interstate dispersion, as exemplified by the beet leafhopper, discussed below.

In an attempt to determine the overwintering quarters of the potato leafhopper, *Empoasca fabae* (Harr.), Washburn (1910) presented data giving the numbers of leafhoppers in alfalfa fields at distances from apple orchards. The data from the different days' collections were combined for use in drawing a single curve (fig. 19A).

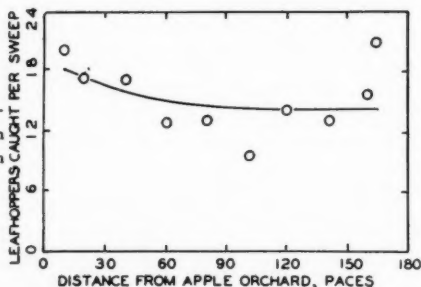


FIG. 19A.—Incidence of the potato leafhopper at distances from apple orchards (data from Washburn).

Slightly more (3.74 based on curve values) leafhoppers were found nearest the orchard. A distance of 155 paces, however, was required to show the difference. Close agreement of the observed and the curve values is lacking.

The source of the beet leafhopper, *Eutettix tenellus* (Bak.), constituted for years a problem because of its sudden appearance miles from the known breeding grounds. The problem was solved through dispersion studies by which it is now generally accepted that the insects disperse from the breeding grounds in

the Southwestern States to the more northern field crops. Definitive evidence on dispersion of this species up to 450 miles constitutes the extreme range for distance data found in the entomological literature. Further evidence of *E. tenellus* dispersion is presented under the heading Kingdom Vira.

Fulton and Romney (1940) collected beet leafhoppers from plants at various distances from a convenient point in the breeding area up to 450 airline miles away. The time-honored sweep net method was used in the collecting and sampling procedure. A unidirectional northward dispersion was indicated by these collections. Two curves were drawn from the number of leafhoppers per 100 sweep-net strokes collected at points from (1) the Nevada-Utah area northward, and (2) the Nevada-Utah breeding area into Colorado (19B).

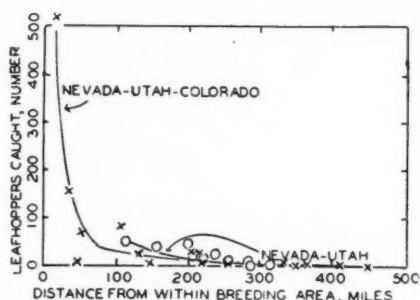


FIG. 19B.—Incidence of the beet leafhopper from within the known overwinter breeding area (data from Fulton and Romney) as determined by the sweep net method.

An interesting similarity of the curves is their tendency to intersect near the zero point at about 300 airline miles from the apparent source within the Nevada breeding area. The observed values lack as close alignment with the curves as might be desired. A mean annual dispersion rate to give expected distances of dispersion could be obtained by yearly repetitions of leafhopper collections.

The chloroform-extractive method of measuring dispersion of the beet leafhopper, as reported by Fulton and Romney (1940), gave data from which two regression curves were drawn (19C).

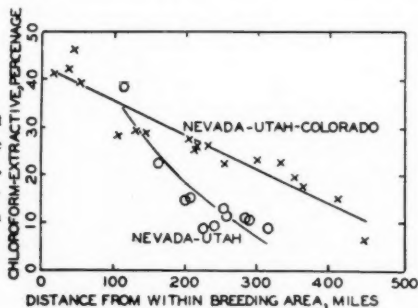


FIG. 19C.—Incidence of the beet leafhopper from within the known overwinter breeding area, as determined by the chloroform-extractive method (data from Fulton and Romney).

Less extreme variations were reported by the authors for the chloroform-extractives method than for the sweep-net method which appear to be substantiated by the closer agreement of observed and curve values in figure 19C than in figure 19B. The possible source, distance dispersed, or age of insects may be determined qualitatively by the chloroform-extractives method but comparative quantitative numbers of them must necessarily be obtained by some other sampling method. Qualitative determinations, however, are valuable and may be required for a balanced program of dispersion research.

Chermidae.—Dispersion of the blackberry psyllid, *Trioza tripunctata* Fitch, from overwinter quarters in pine and spruce woodlands was found by Peterson (1923) to infest most heavily the rows nearest the woodlands (fig. 19D).

The ten outside rows were most heavily infested. The infestation decreased most heavily over the outside four rows. Zero infestation was not observed in the field at any distance. The curve, however, shows a low level of infestation near the twelfth row from the border facing the woodlands.

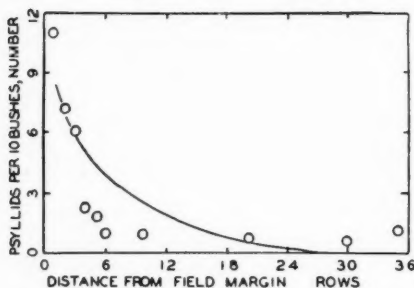


FIG. 19D.—Dispersion of the blackberry psyllid (data from Peterson).

Coccidae.—Data on black scale, *Saissetia oleae* (Bern.), dispersion were given by Quayle (1916), expressed in number of insects per sheet of adhesive. Sheets were placed in different situations and at different distances from infested trees. Two curves were drawn; one from sheets given a western exposure from an infested orchard, and the other from sheets exposed at distances from an artificial tree or bouquet (fig. 20A).

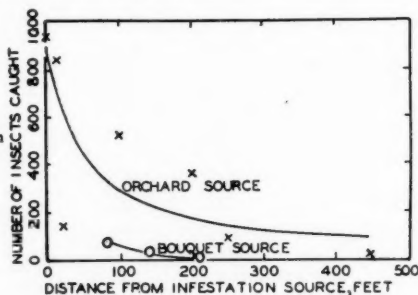


FIG. 20A.—Black-scale dispersion (data from Quayle).

Rather wide dispersion of the species is shown which is very interesting in view of its lack of wings. These experiments gave information in explanation of scale infestations on trees shortly after control work was practised and where infested trees were not far distant. The example illustrates how uncared-for trees in nearby property may endanger and increase the cost of controlling insects on cared-for productive trees.

Buprestidae.—Numbers of roundheaded apple-tree borers, *Saperda candida* Fab., were released in an orchard by Brooks (1920). Later borer larvae were counted at distances from the release point. These borers were progeny of the released borers, and perhaps also by others. The number of borers decreased, however, with distance increase. Graphic results are shown in figure 20B.

The rate of decrease for egg deposition was rather rapid for six rows and then slowly to 16 rows, as shown by the curve. The observed decrease ended at 12 rows then began to increase. This increase may be attributed to dispersion of borers from outside the orchard or to marginal influences, according to the author.

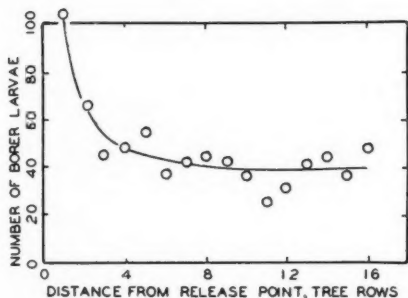


FIG. 20B.—Incidence of round-headed apple-tree borer larvae at distances about the release point of adults (data from Brooks).

Cucujidae.—In a study of rice insects in storage Douglas (1941) reported that dispersion of the flat grain beetle, *Laemophloeus minutum* (Oliv.), dispersed to rice shocks from several probable sources. All data, however, were combined for drawing a curve (fig. 20C).

A distance of 400 feet showed reduced infestations. Removing rice to more

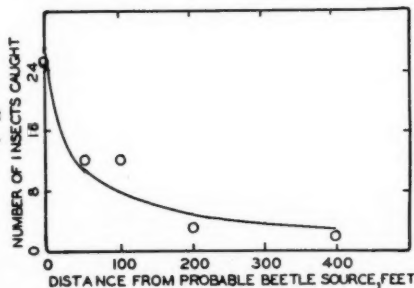


FIG. 20C.—Dispersion of the flat grain beetle (data from Douglas).

remote distances from storage bins would be localized control of a practical nature.

Coccinellidae.—Very small portions of liberated convergent ladybeetles, *Hippodamia convergens* Guerin, were recovered by Davidson (1925) in his dispersion study. Classification of the recoveries from the three experiments into distance classes was made in order to draw a curve (fig. 20D).

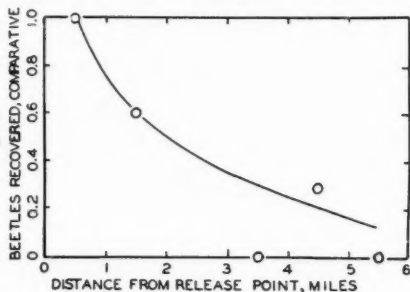


FIG. 20D.—Dispersion of the convergent ladybird beetle (data from Davidson).

The dispersion of this aphid predator is shown to cover a distance range in terms of miles. Over 11 per cent as many beetles were recovered at 5.5 as at 0.5 miles from the release point, according to the curve values. The curve slope is comparatively slight as compared with many dispersion regressions.

This exemplifies the often laborious task of recovering liberated insects. Any method, therefore, as for example the use of statistical methods, which could utilize the few recoveries would result in more efficient research.

Scarabaeidae.—Horizontal dispersion of Japanese beetle larvae, *Popillia japonica* Newm., from the release point in a bin of growing wheat was found by Hawley (1934) to be restricted to a few feet, over a 37 day period. Two inches were added to each of the given distances in compensation for the "more than" of each given distance for the drawing of a curve (fig. 21A).

Half the recovered larvae were within about two feet of the release point. Eight feet was the maximum dispersion.

No dispersion data relative to the adult Japanese beetle were located.

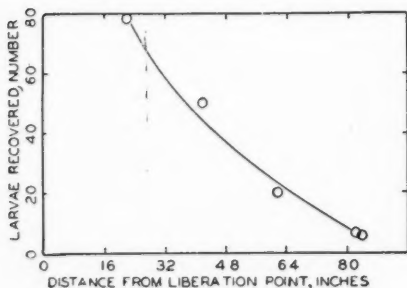
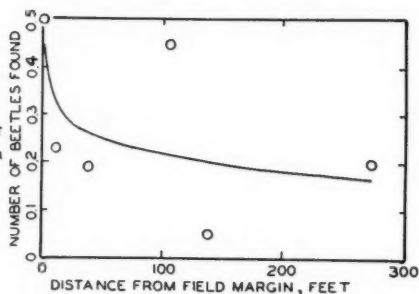


FIG. 21A.—Dispersion of Japanese beetle larvae (data from Hawley).

Chrysomelidae.—The cucumber beetles, *Diabrotica duodecimpunctata* (F.) and *D. vittata* (F.), considered rather "strong fliers," were studied in their dispersion movements by Bissell (1939) and Dudley and Searles (1923). Two phases of beetle activities, (1) entrance into hibernation quarters, and (2) dispersion after having been caught, dyed, and released, are represented. The results from Bissell's work (1939) showing *D. duodecimpunctata* insects present in overwinter quarters were used for illustrating one phase of beetle activity (fig. 21B).

FIG. 21B.—Incidence of cucumber beetles about field margins (data from Bissell).



Less than one-third as many beetles were calculated to have entered hibernation at 273 as at 1 foot. The beetles reported in this work dispersed without having been caught or caged. It is well to understand this fact if comparisons are attempted with the data in which the insects were handled or enclosed. Any increase or decrease of distance dispersed resulting from caging and handling, or freedom of dispersion unhampered, is unknown.

A very small portion (0.18 per cent) of the marked and liberated *Diabrotica vittata* beetles reported by Dudley and Searles (1923) was recovered. The results given, however, were used for drawing a curve (fig. 21C).

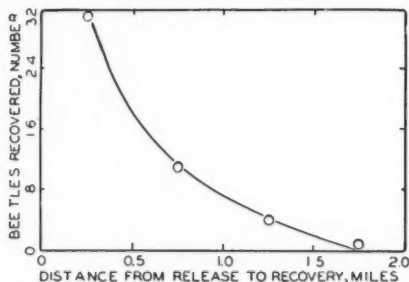
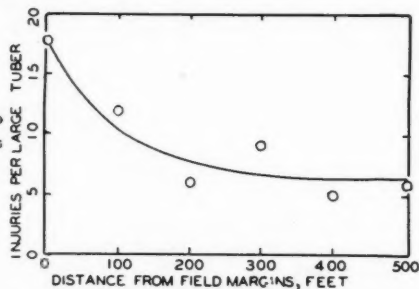


FIG. 21C.—Dispersion of marked cucumber beetles (data from Dudley and Searles).

Fair agreement of the curve with the observed numbers is illustrated. Since no beetle was recovered at the 1.75 mile class compared with 31 at the 0.25 mile class, the limit of dispersion was undoubtedly more distant than the recovery at the greatest distance.

A study of the incidence of tuber injuries made by larvae of the potato flea beetle, *Epitrix cucumeris* (Harr.), by Wolfenbarger (1940), showed that more injuries were found within 100 feet of the margin of fields than at 200 or more feet distance (fig. 21D).

FIG. 21D.—Incidence of potato flea beetle injuries to tubers (data from Wolfenbarger).



The incidence of injuries shown was influenced by host plants growing outside the potato fields, among which more beetles were shown to hibernate than in the fields. Observations showed that leaf injuries were also more numerous near field margins than at more remote distances. Close agreement of observed and calculated values is lacking, caused probably by lack of repetition.

Mylabridae.—Wide variations were found in pea weevil, *Bruchus pisorum* L., infestations by Larson et al. (1933). The heaviest infestations were usually found nearest the beetle sources, hibernation quarters and low places. Average infestations for each distance class were used for drawing a regression curve (fig. 22A).

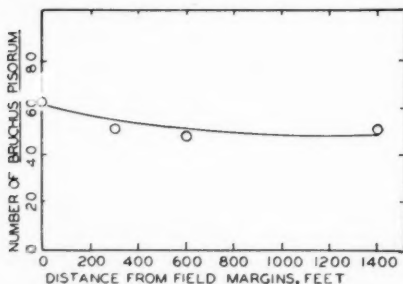


FIG. 22A.—Incidence of pea weevil infestations in field margins (data from Larson et al.).

A reduction of near 12 per cent is shown within 400 feet of the end of a field, then reductions of small magnitude extend to 1400 feet.

Forested areas, hibernation quarters of the pea weevil, *Bruchus pisorum* (L.), were shown by Wakeland (1934) to influence pea weevil populations by dispersion. From the data given a curve was drawn to show the rate of influence as measured by distance (fig. 22B).

A distance of four miles showed a curve difference of 11.4 weevils. A low weevil density is approached at five miles from forested areas.

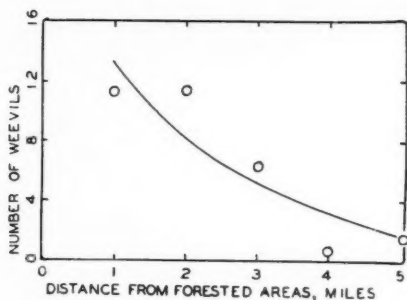


FIG. 22B.—Dispersion of the pea weevil from overwinter quarters (data from Wakeland).

Two distance ranges are noted in these two references. The shorter distance range of from 0 to 1400 feet would not show much reduction if a longer distance range of five miles illustrated a more definite relationship.

Curculionidae.—Seasonal catches of the cotton boll weevil, *Anthonomus grandis* Boh., illustrates another example (as does the injury incidence of potato tubers in figure 21D by Wolfenbarger) in which the relationship of distance from hibernation quarters was determined by the number of beetles that were progeny of the overwintered beetles. The data from Gaines' (1932) work, except the $1\frac{1}{4}$ mile distance, were used to draw a curve. The $1\frac{1}{4}$ mile distance was excepted because late planted cotton, according to the author, influenced the number of beetles caught at that distance. The regression curve is given in figure 22C.

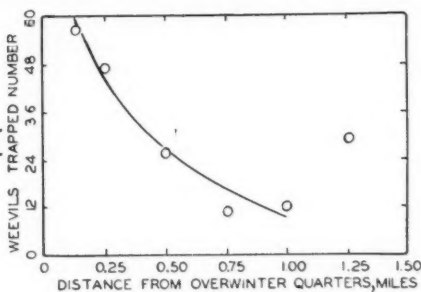
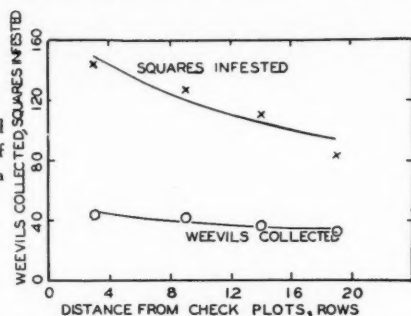


FIG. 22C.—Cotton boll weevil dispersion from overwinter quarters (data from Gaines).

Less than 15 per cent as many beetles were trapped at one mile as at $\frac{1}{8}$ mile, determined by the curve values. The curve and the observed numbers have close agreement. Attention given to planting cotton at more remote distances from hibernation quarters or of destruction of hibernation quarters would appear to afford some relief from weevil infestations.

In studies of the cotton boll weevil, *Anthonomus grandis* Boh., control by picking operations, Coad and McGehee (1917) collected more insects and found more infested squares on the rows next to check, or unpicked plots, than on more distant rows. Curves were drawn for each of these two factors and are shown in figure 22D.

FIG. 22D.—Cotton boll weevil dispersion, and of incidence of infested cotton squares (data from Coad and McGehee).



The regression curves show that greater differences existed between infested squares, at the nearest row compared with the more distant rows, than of beetles collected. Relative relationships between beetles collected and infested squares are quite clear. The observed and curve values show close agreement.

Cotton plants depopulated in insect populations by picking beetles tend to become re-populated subsequent to picking. The steeper slope of the curve of infested squares suggests that the rows nearest the check plots were affected more than the beetle populations. This may be explained, perhaps, by increases in the number of beetles between successive pickings but greater increases at the margins than in the more distant rows.

The dispersion of overwintered cotton boll weevils was studied by Reinhard and Thomas (1933). In this work marked beetles were released and observed by daily movements for 14 days by sexes. Since a more rapid rate of dispersion was reported for the females than for the males, and because of the interest involved curves were drawn for each sex (fig. 23A).

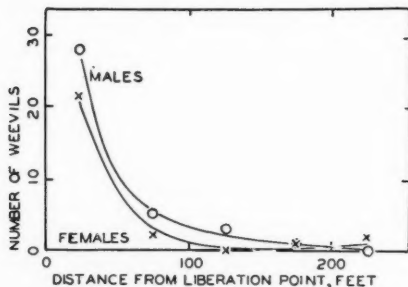


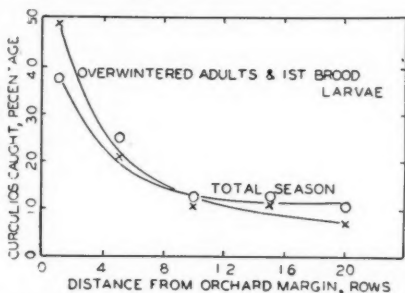
FIG. 23A.—Cotton boll weevil dispersion (data from Reinhard and Thomas).

Rapid initial, and similar rates of dispersion to near 75 feet from the release point are indicated for both sexes. Fair agreement of the observed values with the curves is shown.

Distribution of the plum curculio, *Conotrachelus nenuphar* (Herbst.), in orchards at distances from woodlands was reported by Stearns and Haden (1932), and by Stearns et al. (1935). The distribution resulted from the dispersion of overwintered beetles and from the dispersion of their progeny

which together make up the total seasonal distribution. Two phases are illustrated, therefore, and two curves were drawn (fig. 23B).

FIG. 23B.—Plum curculio dispersion in orchards at distances from woodland margins (data from Stearns and Haden for overwintered adults and first-brood larvae, and Stearns et al. for total season).



The most plum curculios were found on peach trees bordering woodlands, the most favorable hibernation quarters. A steeper curve resulted from data illustrating overwintered adult and first brood grub abundance. Five-row distances greatly reduced the infestations. At 20-row distances the curves were less sloping. From these curves it appears that the progeny of overwintered adults do not disperse widely through the orchards from their origin. The authors observed that, although most curculios were concentrated in greatest numbers at the margins and the distance into the orchards increased the beetle abundance decreased to low levels, the distribution remained somewhat equal in the orchard beyond the 20-row distance.

Marked plum curculios released by Steiner and Worthley (1941) were later recaptured by jarring trees at distances from the release point. Data on the number of days elapsed between release and recapture were also presented by these authors. Two curves were drawn to illustrate the two relationships (fig. 23C).

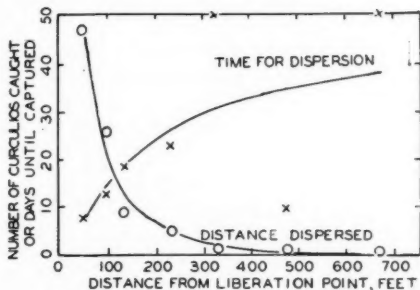


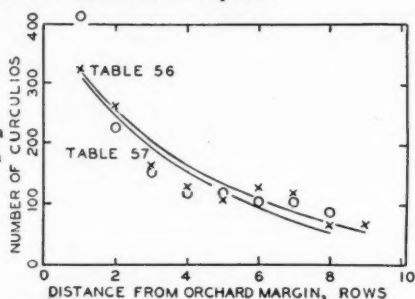
FIG. 23C.—Plum curculio dispersion (data from Steiner and Worthley).

Most of the curculios, based on the curve values, were taken within 94 feet of the release point. One beetle was recaptured at 671 feet distance. Rather close agreement of observed and curve values is shown.

The number of days elapsed between release and recapture of the beetles affords an interesting relationship. An upward sloping curve, i.e., an increase

of time with increase of distance, is expected and shown in figure 23C. Whether the beetles dispersed directly to the trees on which they were taken, or whether they moved intermittently within ambits until they were recaptured is not known. It seems likely, however, that dispersion occurred by intermittent, perhaps irregular, movements until the beetles were recaptured.

Fig. 23D.—Incidence of plum curculio infestations (data from Snapp).



In an extensive series of observations on the plum curculio, *Conotrachelus nenuphar* (Herbst.), Snapp (1930) showed how much more concentrated the curculios were on the border rows. The beetles hibernated about the peach orchards in forests, asparagus beds, fields, and other places. Data in several tables, obtained from several locations and under different conditions, showed similar rates of decrease in beetle distribution, although more curculios were found on all rows in some locations than in others. The data from two tables were used for drawing two curves indicative of the rates of decrease of beetles from the border rows inward (fig. 23D).

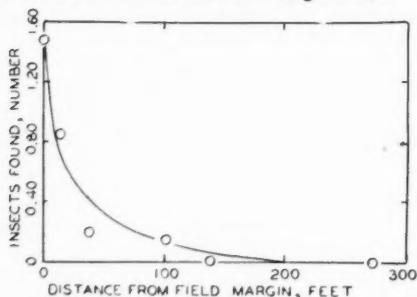


Fig. 23E.—Incidence of cowpea weevils about fields (data from Bissell).

Eight row distances reduced the infestations a third as much as at one row distance from the orchard margin. The two curves appear to illustrate the usual distribution of plum curculios in orchard margins.

Winter quarters of the cowpea weevil, *Chalcodermus aeneus* Boh., were shown to be more abundant about cowpea fields, with more beetles nearer field margins than at more distant points from the fields. The data by Bissell (1939) were used for drawing a curve to show the abundance of beetles as related to cowpea fields (fig. 23E).

Most of the beetles were within 100 feet of the fields. At a distance of 273 feet from the field border no beetle was found. Rather close agreement of the curve with the observed values is shown. The practicability of burning as a local control measure, to a distance of 100 feet, was suggested by the author.

A greater portion of liberated strawberry crown borer, *Tyloclerda fragariae* (Riley), beetles was recovered from distances nearer strawberry beds than at more remote distances, as shown by Ritcher (1939). These beetles, which must crawl owing to their wing vestiges, were released at different times and distances from the strawberry bed. Percentages of the released beetles that reached the strawberry bed and the distances of the release points from the beds were used for drawing a regression curve (fig. 24A).

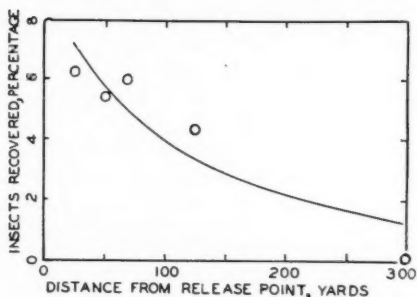


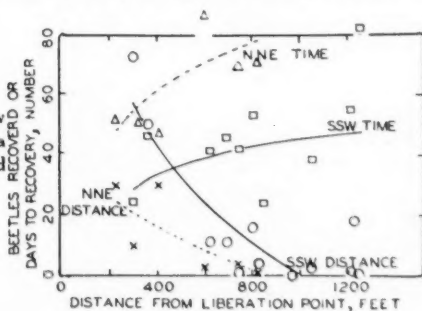
FIG. 24A.—Dispersion of the strawberry crown borer (data from Richter).

The percentages of the beetles that reached the bed were 6.01 and 1.15 at 25 and 300 yards, respectively, according to the curve. A practical application of the experiment was to determine the distance at which to plant new beds with relation to the old.

The semi-logarithmic formula was used to calculate the curve values, although the regular formula $E = a + b(x)$ gives figures which "fit" better the observed values.

Dispersion of New Guinea sugar cane weevils, *Rhabdocnemis obscura* Bdv., was studied by Van Zwaluwenburg and Rosa (1940). These workers reported on distance covered, in feet, and the time, in days, between liberation and

FIG. 24B.—Dispersion of the New Guinea sugar cane weevil (data from Van Zwaluwenburg and Rosa).



recovery points, for both males and females. No significant differences existed between directional trend of sexes. Differences between "up-wind," NNE, and "down-wind," SSW, both as to distances and time intervals, however, were significant. Four curves were drawn to show these different relationships (fig. 24B).

Dispersions "down-wind" began with a higher initial number of recoveries that continued to greater distances than "up-wind" dispersions. At between 800 and 1000 feet from the liberation point few beetles were recovered. A trend is seen in these curves for reciprocity to exist between the number of beetles recovered and distance dispersed as related to the time required for dispersion.

The maize billbug, *Calandra maidis* (Chittenden), a pest of corn, was shown by Cartwright (1929) to infest the border rows more seriously than those in the center of the field. Data collected on May 29 and June 5 were presented in distance terms of rows. Two curves were drawn to show the results (fig. 24C).

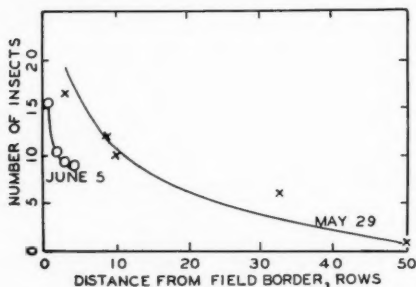


FIG. 24C.—Incidence of maize billbug infestations (data from Cartwright).

The infestations were more severe on the five marginal rows and diminished to the fiftieth row. Localized control measures applied to the border rows would appear practical.

In a study of rice insects Douglas (1941) reported on dispersion of the rice weevil, *Sitophilus oryzae* (L.). The comparatively few data, which by statistical analysis showed no significant differences between localities, were combined for drawing a single curve (fig. 24D).

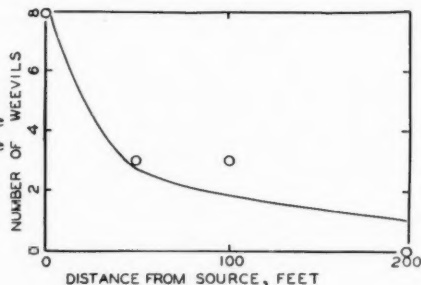


FIG. 24D.—Concentration of the rice weevil about its source (data from Douglas).

The slope of the curve is comparatively slight. Since the observed numbers of insects were small one might question what form the regression would take if the infestations were more dense, or if there were more observations.

Scolytidae.—This family of beetles is ordinarily considered from an economic viewpoint as important shade or forest tree insects. The determination of dispersion characteristics for species would indicate whether local or widespread control measures would be more effectively employed.

The incidence of twig crotch injuries made by the smaller European elm bark beetle, *Scolytus multistriatus* Marsh., has been reported by Collins (1938), Wallace (1940), Wolfenbarger and Jones (1943), and Wadley and Wolfenbarger (1944), in relation to spreading of the organism causing the Dutch elm disease. The paper by Wadley and Wolfenbarger (1944) presented in some detail data on twig crotch wounds. Especial attention was given to the consideration and development of statistical formulae with reference to regression. The two curves showing twig crotch injury incidence are given in figure 25A.

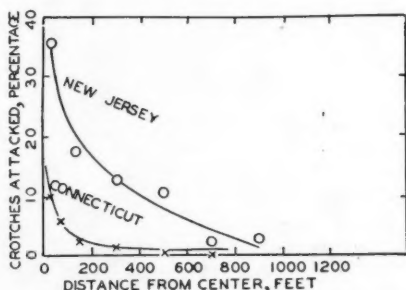


FIG. 25A.—Incidence of smaller European elm bark beetle injuries about sources of the beetle (data from Wadley and Wolfenbarger).

Percentages of injuries declined rapidly to 600 and 800 feet after which they declined slowly. Low incidence became lower but did not reach zero except at unknown distances. Differences between directions were insignificant.

Wallace (1940) reported on the incidence of twig crotch wounds by *Scolytus multistriatus* Marsh. about the emergence point from which a curve was drawn (fig. 25B).

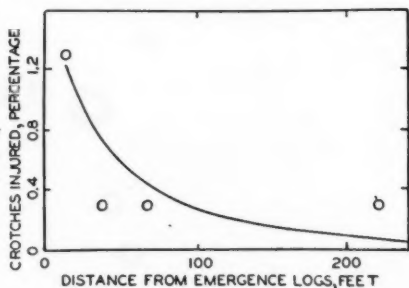
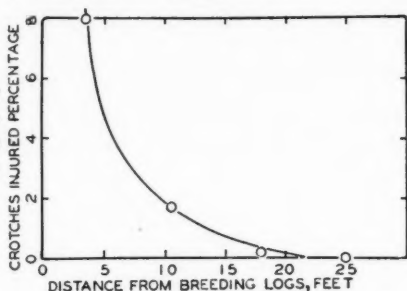


FIG. 25B.—Incidence of smaller European elm bark beetle injuries about sources of the beetle (data from Wallace).

A low level of injuries was reached at near 225 feet from the emergence logs, or source.

The above discussions refer to twig crotch incidence wounds made by beetles in their dispersion activities. Wallace (1940) and Wolfenbarger and Jones (1943), however, presented results of observations on convergence activities (the relationships of distance from trap or logs where the insects were coming to breed.) Wounds were counted at distances from these logs. A curve was drawn from the data given by Wallace (1940) (fig. 25C).

FIG. 25C.—Incidence of smaller European elm bark beetle injuries about convergence points of the beetles (data from Wallace).



Few wounds were found to have resulted from beetles converging to logs in condition for breeding, and these were restricted to short distances from the logs. Zero injuries were reached, computedly, at near 13 feet from the logs. Low percentages of crotch wounds were also observed by Wolfenbarger and Jones (1943). They reported that 1.0 and 0.5 per cent of the crotches at 6 and 25 feet, respectively, from breeding logs could be expected to have wounds.

Recorded observations on the number of maternal galleries in trap trees at different distances from known sources of beetles were given by Whitten (1938) and Wolfenbarger and Jones (1943). The most galleries per unit area of attractive breeding logs were found in trees nearest the beetle sources. Two regression curves were drawn from these data (fig. 25D).

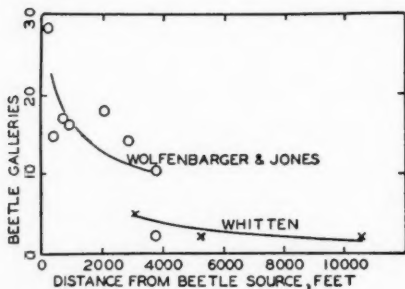


FIG. 25D.—Incidence of smaller European elm bark beetle maternal galleries at distances from the beetle source (data from Wolfenbarger and Jones and from Whitten).

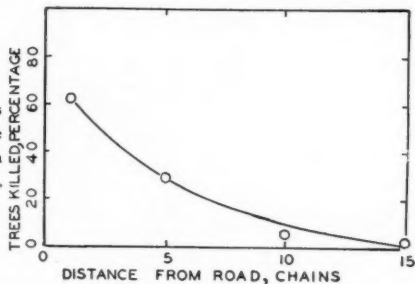
Dispersion of the smaller European elm bark beetle is expressed in terms of miles for the location of breeding material. The curve drawn from the data

given by Wolfenbarger and Jones (1943), although lacking close agreement with the observed values, is similar in curvilinearity to that from the data recorded by Whitten (1938). Each curve is, therefore, complimentary to the other and indicates what rate of dispersion may be expected from the beetles seeking breeding logs or trees.

The dispersion activities of *Scolytus multistriatus* Marsh. for breeding, to distances in terms of miles, is very important from the viewpoint of Dutch elm disease transmission. Incidence rates of the disease, shown in figures 6C and 6D, occur in distance ranges of hundreds of feet, as do twig crotch wounds (figs. 26A and 26B). Two distinct dispersion activities (three if it may be accepted that beetles converging on breeding materials may constitute one) are, therefore, indicated for *S. multistriatus* and two (or three) incidence rates of diseased trees may be expected, depending on the beetle activity involved.

Data recorded by Bedard (1939) on the mountain pine beetle, *Dendroctonus monticolae* Hopk., illustrate an example of the influence of trees and slash left by road construction work. The beetles reproduced in the trees and slash so abundantly that a local epidemic was the result. More trees were killed nearest the beetle emergence points (fig. 26A).

FIG. 26A.—Incidence of trees killed by the mountain pine beetle at distances from a roadway (data from Bedard).



At a distance of 15 chains from the beetle source a small portion, 2.3 per cent of the trees was killed, whereas 62.5 per cent was killed at one chain. The results serve to emphasize the importance of clean-up work after construction of roadways, buildings, or other structures following the destruction or weakening of living trees.

Graham (1922) observed that the red turpentine beetle, *Dendroctonus valens* Lec., was attracted to recently cut pine logs although they entered nearby trees and stumps for breeding. The infestations centered about the attractant materials and decreased as the distance from them increased. These data may, therefore, be termed convergence, or combination of dispersion and convergence. The regression curve is shown in figure 26B.

Most of the infestations were within a few hundred feet from recently cut pine logs. At between 300 and 400 feet from the attractant materials the slope of the curve assumes a flattened form.

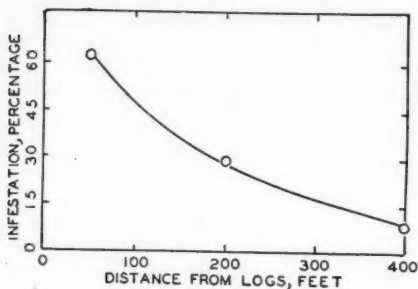
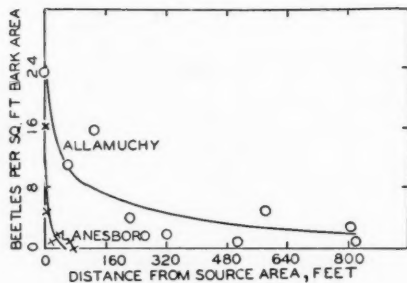


FIG. 26B.—Incidence of tree and stump infestation of the red turpentine beetle at distances from recently cut pine logs (data from Graham).

Data on dispersion of the native elm bark beetle, *Hylurgopinus rufipes* Eich., from the emergence point to living trees were given by Wolfenbarger (1941), in each of two areas. These data referred to late summer and fall emergent beetles having sought hibernation places in living trees. They were collected from two locations: (1) Allamuchy, New Jersey, where great numbers of beetles had emerged from chemically treated trees, and (2) Lanesboro, Pennsylvania, where smaller numbers of beetles had emerged from slash left from mine timber cuttings. Two curves were drawn from these locations (fig. 26C).

FIG. 26C.—Dispersion of the native elm bark beetle to overwinter quarters (data from Wolfenbarger).



Dispersion for hibernation is seen in terms of hundreds of feet when beetle populations are great, and within one hundred feet, perhaps, when the beetle density is low.

These data give some indication of the distance beetles disperse for hibernation. Dispersion of the beetles for breeding is another activity, however, and published data on it are unknown. Field observations by the author suggested that they disperse in terms of miles to find suitable breeding material.

Much of the entomological literature devoted to "insect migration" concerns the Lepidoptera. Colorful parades of graceful flying butterflies and moths are striking in appearance, and the insects are large enough for observations in flight. Members of the order Lepidoptera afford interest and fascination for studies in dispersion. Most of the references are, however, qualitative in charac-

ter. Organized systematic studies which provide definitive data are often lacking, except in reference to economic species.

Gelechiidae.—Dispersion of the anguomais grain moth, *Sitotroga cerealella* (Oliv.), was studied by Simmons and Ellington (1927) by observing infestations of the moths in grain shocks at different distances from storage bins and in different fields. Three curves were drawn, one for each of the years 1924, 1925, and 1926 (fig. 27A).

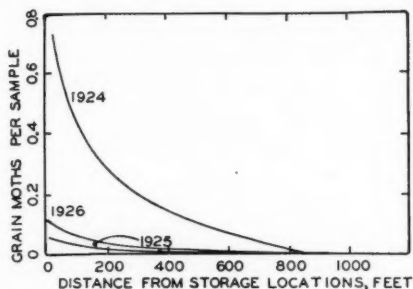


FIG. 27A.—Dispersion of the anguomais grain moth (data from Simmons and Ellington).

Near the 800 foot distance low levels of infestations were found. In the three-year period of observation the heaviest infestations occurred in 1924, the lowest in 1925. Regardless of high or low levels of infestations near the origin of dispersion the 800 to 1000 foot distance is near the point at which the different curves reach low levels of infestation. This distance figure may be utilized for the application of local control measures. The numerous observed values were omitted from figure 27A since the curves are the significant feature and show the incidence of infestation.

Incidence of rice infestation by the anguomais grain moth was reported by Douglas (1941), which covered distances ranging from near the source to 600 feet. Variations between localities were regarded as insignificant and were combined for drawing a single curve (fig. 27B).

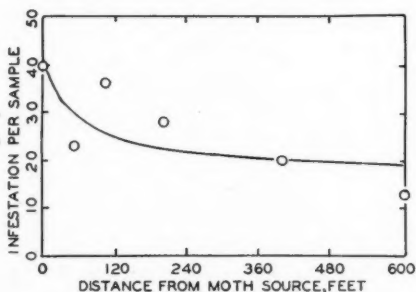


FIG. 27B.—Incidence of rice infestation by the anguomais grain moth (data from Douglas).

The calculated amount of the infestation at the "nearest point," taken as of one foot, was 41.5, and at 600 feet was 19.8, which is a reduction of slightly

less than one-half. Six hundred feet is, therefore, too short to portray the regression of the infestations observed. Close agreement between observed and curve values is lacking.

Tortricidae.—Dispersion studies of the oriental fruit moth, *Grapholita molesta* (Busck), were made by Frost (1931). These moths were marked and released. In trees at different distances from the release point bait traps caught 21 (52.5 per cent) of the released moths. Distances are given in terms of "tree spaces" since no other unit of length was given (fig. 27C).

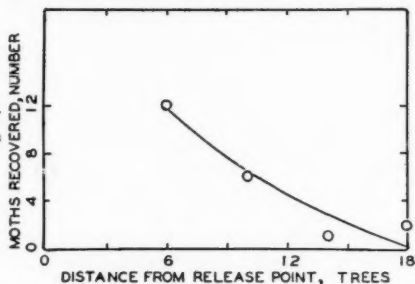


FIG. 27C.—Dispersion of the oriental fruit moth [data from Frost (1931)].

Most moths were recovered at 6 tree spaces from the release point. One moth was recovered at 17.1 and one at 16.6 tree spaces from the liberation point. In consideration of the comparatively meager data close agreement between the observed and curve values is seen.

In a later publication Frost (1933) showed how the oriental fruit moth, *Grapholita molesta* (Busck), dispersed to three points outside of an orchard. Moth traps were placed 100 feet north, one-eighth and one-fourth mile west of an orchard and operated throughout a season. A curve was drawn from the results of the trap catches without reference to directional influences of dispersion (fig. 27D).

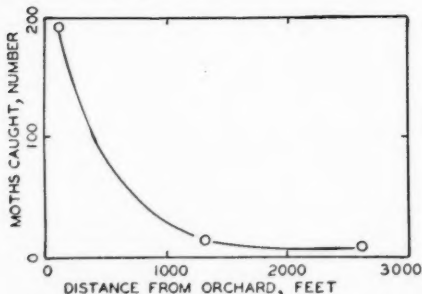
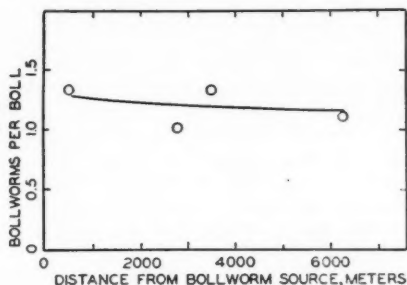


FIG. 27D.—Dispersion of the oriental fruit moth [data from Frost (1933)].

A rapid rate of regression is seen from 100 to 1300 feet after which the curve slope is much reduced. The terminus of oriental fruit moth dispersion was evidently at some distance more remote than the one-fourth mile from the orchard since moths were caught at the most distant point.

Dispersion of the pink bollworm, *Pectinophora gossypiella* (Saund.), an insect which is credited with widespread dispersion powers, was studied by Ohlendorf (1926). A curve drawn from the data indicates a trend of distant dispersion for the species (fig. 28A).

FIG. 28A.—Incidence of pink bollworm infestations (data from Ohlendorf).



The slight slope of the curve to 6250 meters, the extreme distance under observation, indicates only slightly reduced numbers of bollworms. The curve values of bollworms are 1.30 and 1.16 per boll at 1000 and 6250 meters, respectively. These values give indications of the distance range necessary to consider for dispersion of the pink bollworm. Lack of agreement of the observed and the calculated values, however, leaves more information on pink bollworm dispersion to be desired.

In view of the extensive experiments to control the codling moth, *Carpocapsa pomonella* (L.), it might be expected that much information on distances of its dispersion had been determined. Although variations in larval abundances and unequal infestations are recognized in the orchards, and greater concentrations of moths are often found around packing houses or cull dumps, more information is needed on the dispersion activities of this important insect.

Two papers, one by Worthley (1932) and the other by Van Leeuwen (1940), gave data on dispersion of moth adults. Two reports, one by Steiner (1939) and the other by Stultz (1943), indicate distances to which codling moth larvae disperse. The data given by Steiner, however, were not quite suited for drawing a curve.

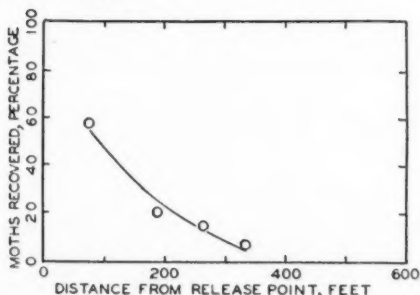


FIG. 28B.—Dispersion of the codling moth (data from Van Leeuwen).

The data given by Van Leeuwen (1940) were obtained by the recovery of moths that had been marked and liberated. Percentages of the total moths recovered within given distances are shown in figure 28B. Over 50 per cent of the moths recovered were within 100 feet, and 15 per cent of the recoveries were made within 250 feet of the liberation points. Fair agreement exists between the observed and the curve values.

Worthley (1932), who also marked and liberated codling moths, recovered over 11 per cent of those released through the use of traps. With the number of moths recovered and the three distance classes taken as of 100, 350, and 600 feet a curve was drawn (fig. 28C). Over 50 per cent of the moths were recovered within 300 feet of the release point. Twenty-five per cent of the moths were computed to have dispersed 600 feet. This is over twice the distance for the same percentage of computed recoveries from Van Leeuwen's data. Closer agreement of the computed with the curve values of moth recovery given by Worthley's data is desirable, although part of the differences may be attributable to the three distance classes.

Dispersion of codling moth larvae was measured by trapping larvae in bur-lap bands at distances from heavily infested apples on an unsprayed tree, recorded by Stultz (1943). The rate of dispersion is shown in figure 28D. Most codling moth larvae pupate within 10 inches of the tree trunk bearing

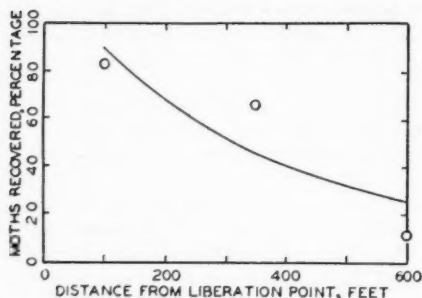


FIG. 28C.—Dispersion of the codling moth (data from Worthley).

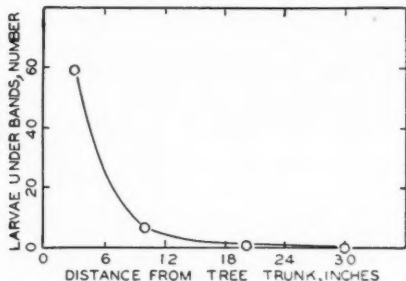
the infested fruit, according to these data. This activity has suggested that the application of control measures at this stage of the insects' life might serve to offer some control.

Pyralidae.—One species of this family, the European corn borer, *Pyrausta nubilalis* (Hbn.), that is of great economic importance in the United States, is well represented by dispersion or convergence data given in five different papers. Three of these papers deal with the adult stage, and two with the larval stage. The publications reporting on the adult stage deal with the convergence response of moths to light and are presented below. These papers, interestingly have the distance interval given in terms of "corn rows." What distance interval exists between corn rows?

The publications by Ficht and Heinton (1939) and Hervey and Palm (1935) are reviewed first. They are comparable in that they (1) contain field data, (2) were attempts to determine control of moths by trapping through

the use of lights, and (3) record observations made on rows one to six, inclusive. No observations on rows more distant than six rows were apparently reported, except as given by Ficht and Heinton (1939) who gave no figure for the sixth row distance from the lights but reported that the infestation

FIG. 28D.—Incidence of codling moth larvae about infested trees (data from Stultz).



was, "normal for the field." The logical explanation appears to be that at distances greater than six rows there was no measurable difference in moth infestation. The two curves representing the observations by Ficht and Heinton (1939) and Hervey and Palm (1935) are given in figure 29A.

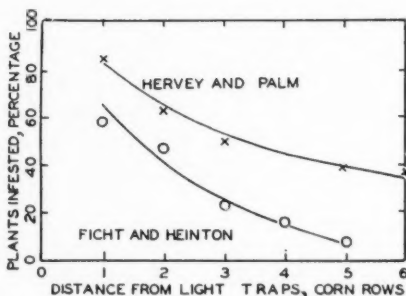


FIG. 29A.—Convergence of European corn borer moths to light traps (data from Hervey and Palm and from Ficht and Heinton).

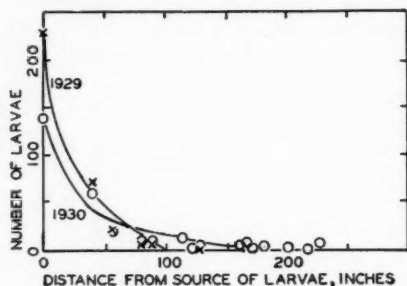
Moth responses were limited to comparatively short radial distances. Comparative percentages of infested plants, based on curve values, over the distance range were one-half as many for the data from Hervey and Palm (1935), and one-eleventh as many for the data from Ficht and Heinton (1939). Light traps were reported by Ficht et al. (1940) to catch more moths on the north-east of corn fields. Traps averaged 401 moths on the first row, 329 on the second, and 253 on the third row from the border.

Dispersion of European corn borer larvae, *Pyrausta nubilalis* (Hbn.) was studied by Neiswander and Savage (1931). Distances between rows and hills were computed as of 40 inches for use in drawing the curves (fig. 29B).

The maximum distances of dispersion observed were 126 and 226 inches for 1930 and 1292, respectively. A more restricted dispersion is shown for

1930 than for 1929. The curve for the 1929 data which were reportedly, "... more nearly normal ..." is characterized by a more gentle slope becoming still more gentle toward the terminus.

FIG. 29B.—Dispersion of corn borer larvae (data from Neiswander and Savage).



Experiments were also conducted by Neiswander and Savage (1931) to determine the effects of density levels of borers at the source or central hill. Three levels of borer density used were 200, 500, and 1000 eggs at the source. Zero infestations were observed at the 2nd, 3rd, and 4th border rows, respectively. Computed zero infestations were reached at 2.1, 2.7, and 3.4 border rows, respectively. Curves representing the three densities have somewhat similar contours. They differ, however, in the tendency of the curves to terminate correspondingly nearer the source with succeeding increases of borer levels. A principle is here involved which warrants further discussion in Part II.

An interesting report on the dispersion of the European corn borer, *Pyrausta nubilalis* (Hbn.), into a field of beets, a less favored host plant, was published by Marshall (1927). The beets adjoined a ruined corn field. A curve was drawn from the distance data and the number of plants entered per hundred (fig. 29C).

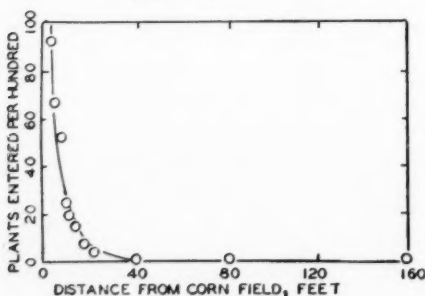
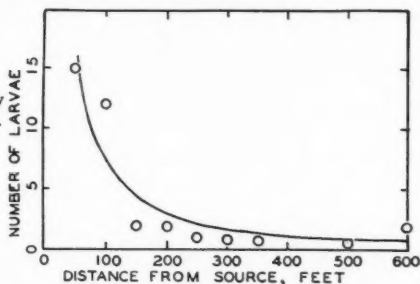


FIG. 29C.—Incidence of corn borer larvae attacks in beets (data from Marshall).

A high incidence of corn borer attack is shown near the edge of the ruined corn field. Beets at distances of more than 40 feet had one per cent of attack, or less. The reaction of borers under stress of low nutritional or less desirable food as measured by dispersion may be illustrated by this report.

Liparidae.—Dispersion studies concerning members of this family are limited to the gypsy moth, *Porthetria dispar* (L.). The frequently quoted work of Burgess (1913) and Collins (1917) can now be regarded as classic in the field of dispersion. Since the female gypsy moth is wingless the larval stage is, interestingly, the one in which its principal dispersion activity occurs. A curve was drawn from the data given by Burgess (1913) involving restricted local distances (fig. 29D).

FIG. 29D.—Dispersion of gypsy moth larvae (data from Burgess).



Fifteen larvae were taken at 50 feet, one at 250, and one at 600 feet from the known source. The curve slopes rapidly to 200 feet, then less rapidly for this passive dispersion stage of the insect. Close alignment of the observed values with the curve is lacking.

The regression curve drawn from Burgess' data (fig. 29D) may be the usual, or expected, dispersion over short or intermediate distances. Collins (1917), however, attempted to learn the unusual or extreme distances of gypsy moth dispersion and found an extreme case of 22 miles. This distance was easterly from the source. The general direction of dispersion appears to have been northeasterly which has been of considerable significance in reference to the distribution of the species.

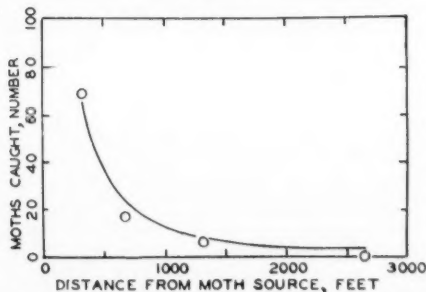


FIG. 30A.—Male gypsy moth dispersion (data from Collins and Potts).

Recovery of liberated male gypsy moths which had dispersed considerable distances was reported by Collins and Potts (1932) (fig. 30A). No moth was recovered at one-half mile distance, although 11, 17, and 69 were reported recovered at $1/4$, $1/8$, and $1/16$ mile, respectively.

In response to mating, some male Lepidoptera are usually considered to disperse for miles to females. In a publication by Collins and Potts (1932) data are given on the distance male gypsy moths were known to disperse seeking the females. A curve was drawn from the data given (fig. 30B).

Males were shown to disperse two miles, and the curve indicates that they go further. Dispersion of the males is more widespread in the search of females than is shown by the experiment on recovery activities.

Minott (1922) conducted some experiments to determine the dispersion of gypsy moth larvae in cranberry bogs. Adhesive coated screens were placed at different distances in the bog from the nearest woodland, presumably source of the larvae, to catch larvae striking them. On account of the comparatively short distances (hundreds of feet) across the irregular, somewhat oval-shaped bog, moth sources may have been other than the woodland nearest the trap screens. From distance data, computed by the scale given in Minott's paper (1922), and the number of moths caught a curve was drawn (fig. 30C).

More gypsy moth larvae were caught nearest the bog margins than at points more distant from the woodland margins. Whatever the source of the larvae may have been a reduction in the number of larvae occurred with an increase in distance from the bog margins. At no point on the bog were there zero catches. Close agreement of the observed with the curve values is lacking, attributable, perhaps, in some measure to the irregular bog margins.

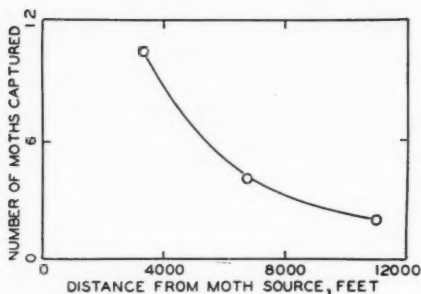


FIG. 30B.—Dispersion of gypsy moth males seeking females (data from Collins and Potts).

Noctuidae.—Brower (1930a and b) marked, released and then recovered part of his liberated *Catocala* moths. On account of the low number of individuals of some species the recovery data from all eight species were used in combination to draw a regression curve. The individual recovery data given by Brower (1930a) were grouped, conveniently, in classes with 25 yard intervals. The two individuals recovered at 1752 yards are not shown in the figure, and were excluded from the formula computations. The rate of dispersion is shown in figure 30D.

Except two, the 34 individuals recovered were located within 375 yards of the release point. There was no evidence indicative of differences in dispersion between species.

Corn plants nearest to the noctuid moth source were shown by Neiswander (1931) to be most heavily infested by *Papaipema nitela* (Guen. (fig. 31A). Low levels of infestation were observed in the fifth and sixth rows from the margin. Marked reductions in infestations over a comparatively short distance range are shown.

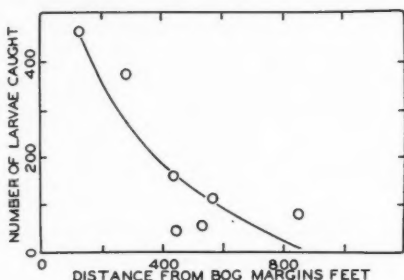


FIG. 30C.—Dispersion of gypsy moth larvae into cranberry bogs (data from Minott).

The convergence of corn earworm moths, *Heliothis armigera* (Hbn.) to lights was reported by Carruth and Kerr (1937). In this case the response was measured by larval infested plants. The method was similar to that reported by Hervey and Palm (1935) and by Ficht and Heinton (1939), for European corn borer. Results of infestation as affected by three different light traps, 25 and 60 watt mercury vapor, and 75 watt tungsten lamps are given. The "left" and "right" directions were summed and averaged for each distance class. Three curves were drawn, one for each light source (fig. 31B).

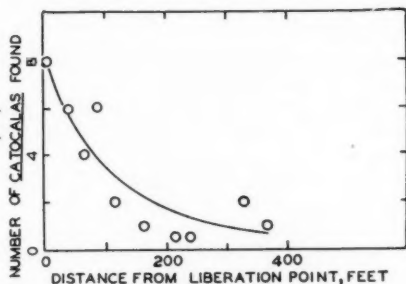


FIG. 30D.—Dispersion of *Catocala* moths (data from Brower).

The infestation convergent on the 25 watt lamp source showed only a slight slope, indicative of almost as much infestation at 10 as at the 1 row distance. Very close agreement of the observed with the curve values is shown for the 25 watt lamp. More marked convergence is seen for the two more intense light sources, about $\frac{1}{3}$ more. Evidently the populations of moths were affected little by the 25 watt lamps and infested the area almost equally, while the stimuli afforded by the more intense light sources affected the regular moth activities.

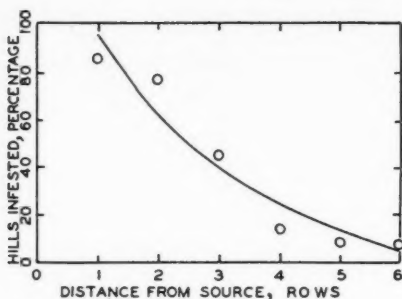
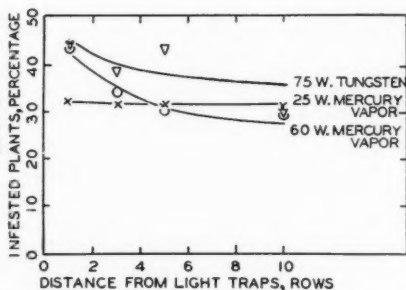


FIG. 31A.—Incidence of corn infested by *Papaipema nitela* (data from Neiswander).

FIG. 31B.—Infestation of corn by corn earworm near light traps (data from Carruth and Kerr).



Species of the highly important order Diptera have been the objects of some splendid studies on insect dispersion. Two papers on the housefly, *Musca domestica* L., by Bishopp and Laake (1919) (1921), and Parker (1916) are so widely quoted that they can be called classics. Extensive experiments were reported in considerable detail by these authors, although extensive results have since been reported by others.

Culicidae.—Recoveries of two lots, 11 and 21 (2.75 and 0.99 per cent, respectively) of 400 and 2130, respectively, of stained anopheline mosquitoes were reported by Adams (1940). Two species, *Anopheles funestus* Giles and *A. gambiae* Giles, were used in these experiments. The data were conveniently grouped in classes with one-half mile intervals for drawing a smoothed curve (fig. 32A).

Less than one-half as many mosquitoes were recovered at 2.75 as at 0.25 miles from the liberation points. Rather wide variations between the observed and the curve values are shown. The semi-logarithmic formula is used for calculating the curve values although the regular formula, $E = 7.7333 - (1.6000)(x)$ appears to give a better "curve-fit."

Kumm (1935) who captured 23 of 616 (3.7 per cent) stained and liberated *Anopheles* mosquitoes caught 18, 2, 0, 0, 0, and 3 within 50, 50-100, 100-200, 300-400, and over 400 yards distance, respectively, from the release point.

Since other and more extensive data are given for *Anopheles* no curve is drawn for these data.

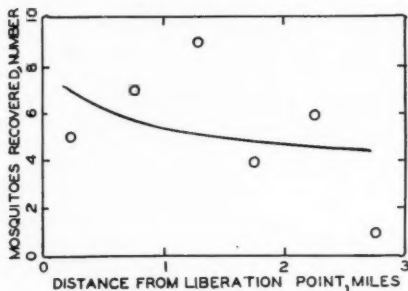
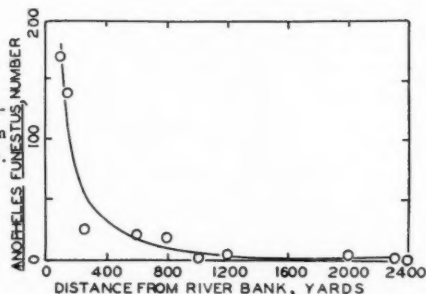


FIG. 32A.—Dispersion of anopheline mosquitoes (data from Adams).

FIG. 32B.—Incidence of *Anopheles funestus* at distances from a river (data from de Meillon).



Liberations of several anopheline species with subsequent recoveries of many liberated specimens were reported by Ave Lallemand et al. (1931). In as much as so few recoveries were made of several species that the data fail to show any species trend the data were summarized by combination of all specimens recovered at each of the different distances and are given as follows:

Recovery distance (yards).....	220	275	330	440	500	550	600	660	880
Mosquitoes recovered (number)....	13	10	3	2	1	6	1	2	6

According to these figures a low level of anophelines is reached at about 500 yards. There are evident fluctuations in the data which may confuse the form of curve that might be expected from more extensive data collected under the same conditions.

In the Transvaal decreasing numbers of *Anopheles funestus* Giles were found by de Meillon (1934) as the distance from the river increased. The rate of decrease is illustrated for the distance range of from 100 to 2400 yards (fig. 32B).

A comparatively steep decline in the number of *Anopheles funestus* is shown. At 1000 yards distance a low level of *A. funestus* was found, indicative of rather restricted dispersion for the species.

Data on dispersion of the efficient malarial vector *Anopheles gambiae* Giles in Rhodesia were given by de Meillon (1937). The eight recovered of the 1500 liberated mosquitoes were placed in distance classes the mid-points of which were 0.75, 1.25, 1.75, and 2.25 miles (fig. 32C).

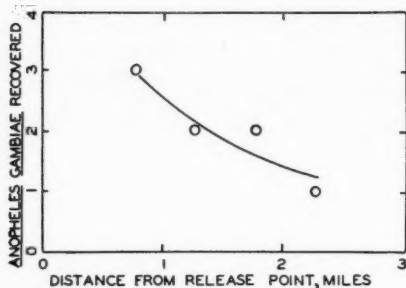


FIG. 32C.—Dispersion of *Anopheles gambiae* (data from de Meillon).

One of eight recovered mosquitoes was taken at 2.25 miles. The curve representing *Anopheles gambiae* is not too unlike those of certain other species. A suggested difference is that it may have comparatively greater distance involved. Curves drawn from a few data do not warrant great confidence.

Dispersion studies of *Anopheles quadrimaculatus* Say and incidence of malaria were reported by Smith et al. (1941). The methods of dispersion study used were the liberation of stained mosquitoes in early experiments and the collection of mosquitoes at distances from impounded waters, apparent source of the insects, in later experiments. The latter method appears to have given the more praiseworthy results, although no evidence of harmful results was

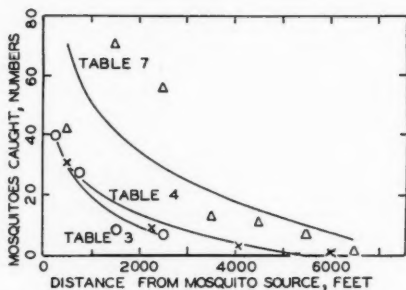


FIG. 32D.—Dispersion of *Anopheles quadrimaculatus* (data from Smith et al.).

apparent from staining the insects. A 6,000 foot distance was taken for the "5,281 or more" of table 4, and a 6,500 foot distance was taken for the "6,000-up" of table 7, otherwise the mid-classes of the distance intervals were used for drawing the regression curves (fig. 32D).

Similar rates of regression of mosquito abundance on distance are shown for the different insect collections. Higher initial mosquito populations gener-

ally indicate higher terminal abundances or more distant dispersions. The dispersion range of *Anopheles quadrimaculatus* is shown to extend thousands of feet. One mile distance from the source, as indicated by Smith et al. (1941), appears to be a practical working distance radius for control measures. At one mile distances low levels of populations became existent.

Suspecting that the usually considered one mile radial distance for anti-malarial mosquito control work might not hold for very dense populations of *Anopheles quadrimaculatus* Say, Huffaker and Back (1945) reported on dispersion of this species. Local conditions favored an investigation around sources of dense populations of *A. quadrimaculatus*. The numbers of mosquitoes in cattle barns and sheds, and also in nail kegs were counted at distances from the breeding areas (fig. 32E).

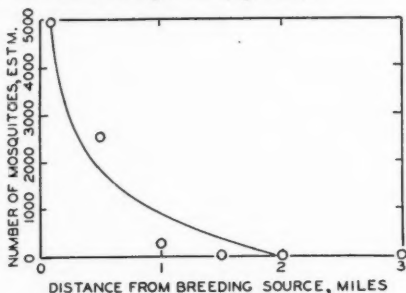
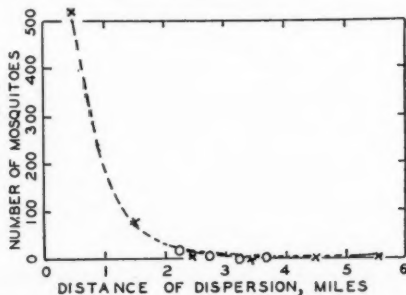


FIG. 32E.—Dispersion of *Anopheles quadrimaculatus* (data from Huffaker and Back).

Rapid decreases in the numbers of mosquitoes were observed to one mile distances and much less rapid decreases to three miles. It was concluded from the data given that, as had others from their studies, one mile distances covered the most significant portions of the dispersion range of the malarial mosquito. The curve, which lacks close agreement with the observed values indicates considerable dispersion to somewhat more than one mile.

FIG. 32F.—Dispersion of *Anopheles quadrimaculatus* [data from Eyles et al. (1945)].



In their latest studies on the malarial mosquito Eyles et al. (1945) have given data from which two *Anopheles quadrimaculatus* dispersion curves were drawn. One curve covers a distance range of 2.00-3.99 miles while the other

covers a range of 0.5 to 6.0 miles (fig. 31F). In the first instance mosquitoes were released, then recovery attempts were made to recapture any released specimens, while in the second instance data from more detailed population studies were taken about an area of more intensive mosquito production. Dispersion of the mosquitoes was considered objectively as that in search of food, domestic blood sources.

A more complete dispersion curve is illustrated by the data on mosquito abundance about the area of intensive insect production. A rapid rate of reduction occurs over the 0.5 to 2.5 mile distance range, followed by a very reduced rate. The mosquitoes recovered over the comparatively short and near-terminal distance range segment of 2.00-3.99 miles illustrates an incomplete dispersion curve. The rate of curvature is, however, similar to that of the more complete curve over the same distance curve. The malarial mosquito is shown to disperse under the given conditions to 3.5 or 4.0 miles. Unusually distant dispersions may illustrate frequency behaviors rather than unexpected aberrations.

Incidence rates of malaria were shown by Smith et al. (1941) to cover distance ranges of thousands of feet. These rates are not incongruous with the dispersion rates of *Anopheles quadrimaculatus*, carrier of the malarial parasite. Data for showing these incidence rates were, however, not as procurable nor as extensive as those for showing the dispersion rates of the insects. A figure of 6000 feet was used for the given, "5000 and over," and "5280 and over" distance data, for drawing the curves of malarial infection, and incidence of malaria (fig. 33A).

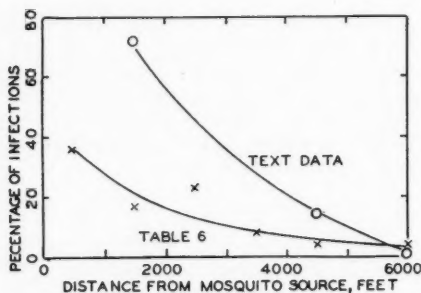


FIG. 33A.—Incidence of malarial infections (data from Smith et al.).

Low incidences of malaria were reached at slightly over one mile distance from the apparent source of the carrier insect. These low incidences, according to the investigators, do "... not mean malaria ended here," but, as is shown by the regression curves, end at some greater distance. The greater portion of the malarial infections is confined, however, within a mile of the mosquito source.

Collections of *Anopheles maculipennis* Meig. mosquitoes were made by Markovich (1941) in the Province of Archangel at different distances from known breeding places along the Dvina river. The mosquitoes were more numerous at the more distant locations in August and September, as they entered diapause. Three curves were drawn (fig. 33B), each from collections

made at different times, and by taking the distances as 0.10, 1.00, and 2.75 miles.

Most mosquitoes were repeatedly collected nearest the river. As the summer advanced, however, the percentages of mosquitoes collected nearest the river

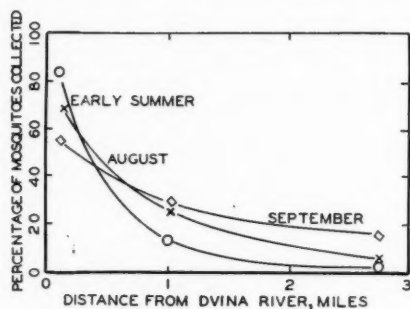


FIG. 33B.—Incidence of *Anopheles maculipennis* about breeding sources (data from Markovich).

decreased in comparison with those taken at the greater distances. There exists, then, a tendency for equalization of mosquito populations over wide areas in the late summer season. This equalization may represent accumulated distribution of mosquitoes in which longevity is a factor and breeding places other than along the river, or combination of factors may also be involved.

Variations in the incidence rates of malaria in the same village were reported by Nikofova (1942), which were attributable to concentration of mosquitoes nearest their hatching place on the Psoll river in Abkhasia. Mosquito dispersion was determined by quantitative determinations of anophelines at distances from the place of hatching, and also by dyeing and later collection of dyed specimens. A graph was presented showing the relative numbers of mosquitoes at distances from the breeding area, and data were given to show the numbers of dyed specimens recovered. The original curves and a curve based on the original data are given to show the dispersion rates obtained in this investigation (fig. 33C).

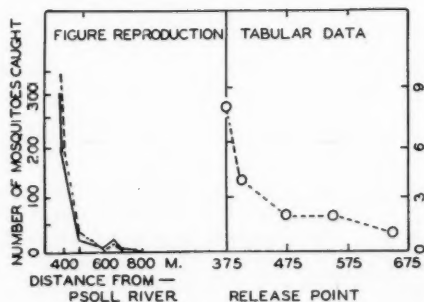


FIG. 33C.—Incidence of mosquitoes nearest their hatching place (data from Nikofova).

The dispersion rates of the species *Anopheles maculipennis* and *A. bifurcatus* were similar. Sharp downward curves indicate rapid rates of dispersion. None of the 17 dyed specimens taken was found farther than 650 meters. Distances of 800 m. ($\frac{1}{2}$ mile) appears to be practical working distances on which to base control operations, unless denser broods of mosquitoes originate at the source.

A diminution in the prevalence of *Plasmodium vivax* and *P. falciparum*, malarial organisms, with increase of distance from Lake Wilson, Alabama, was shown by Watson et al. (1942). Classification and grouping of mosquito producing areas, as indicated by Watson et al. (1942), which has been of value in malarial control, illustrates a usefulness of distance dispersion knowledge. The data from Types II and III, given by Watson et al. (1942), summed and averaged for the distance classes were used for drawing a curve of malarial incidence on distance (fig. 32D).

Approximately one-fourth as much malaria is shown for 0.875 as at 0.125 mile. Very close agreement exists between the curve and observed values, indicative of an adequate sample. Were this disease incidence curve to continue at the exact rate calculated from the data zero *Plasmodium* would be expected at near 1.3 miles from Lake Wilson, while at the Lake shore 7.0 cases might be expected.

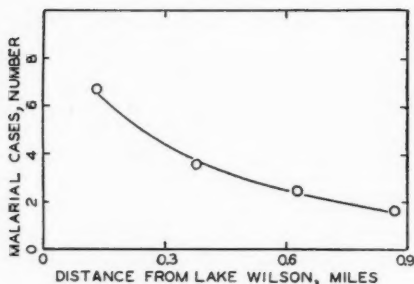


FIG. 33D.—Incidence of *Plasmodium vivax* and *P. falciparum* about Lake Wilson (data from Watson et al.).

Light traps at distances from breeding areas were shown by Bang et al. (1943) to have caught variable numbers of *Anopheles walkeri* Theobald. The numbers of mosquitoes per light trap-hour and the distances from the breeding areas at which they were caught are given as follows:

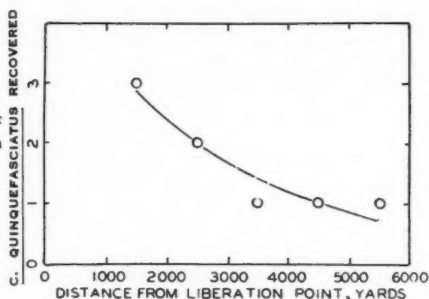
Miles	0	0.5	1.0	1.5	2.0	further
Mosquitoes	2.5	5.7	9.8	2.8	1.4	0.2

No curve is drawn for these data since the rate of dispersion seems indefinite and indecisive. Computation of a formula from these data actually indicated a slight increase instead of a decrease.

Laboratory reared *Culex quinquefasciatus* Say mosquitoes, stained and liberated by Alfridi and Majid (1938) were caught at distances from the

liberation point. Comparatively few specimens were recovered, a not uncommon result observed with many dispersion studies unless many specimens are released. The data on males and females recovered were combined in order to utilize as many units as possible and, in addition, the data were grouped in mid-thousand yard classes. A curve was drawn to show the dispersion rate (fig. 34A).

FIG. 34A.—Dispersion of *Culex quinquefasciatus* (data from Afridi and Majid).



Comparatively little distance effect is evident from nearly a mile to over three miles distance from the liberation point. A rather widespread dispersion rate for *Culex quinquefasciatus* is suggested by this curve segment. An extrapolation of the curve to the origin would number 15 mosquitoes, while at three miles it would number one mosquito. One might question, therefore, what distance might be dispersed by 150,000 mosquitoes at the origin, assuming a similar dispersion rate.

Dispersion of mosquitoes, *Psorophora confinnis* (L.-A.) and *P. discolor* (Coq.), the dark and tan rice-field mosquitoes, respectively, was shown by Horsfall (1943) to be in terms of miles. Two curves were drawn from both sets of data given for *P. confinnis* (fig. 34B).

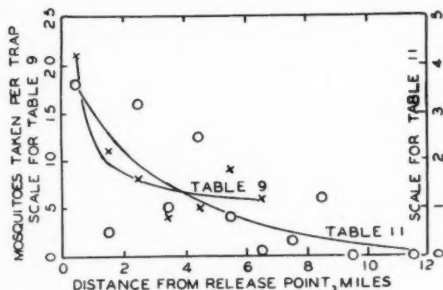


FIG. 34B.—Dispersion of rice-field mosquitoes (data from Horsfall).

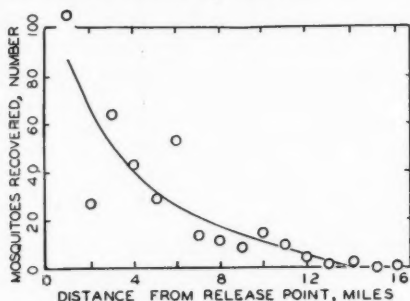
A distance of 11.5 miles diminished almost to zero the expected number of mosquitoes caught, for Horsfall's (1943) table 11. The expected number of mosquitoes at 0.5 mile is 3.72, considered a low initial number compared to

expected zero mosquitoes at 11.5 miles and the expected number at 6.5 miles is 0.69.

The data by Horsfall (1943) in table 9 gave a curve the expected numbers of which were 21.21 and 6.09 at 0.5 and 6.5 miles, respectively. Although there are certain differences in the data in the different tables similar rates of dispersion are considered to have been determined for the species.

The report by Clark (1937) indicated that considerable effort had been expended to determine dispersion of fresh water pest mosquitoes. Dispersion was determined from five experimental releases, at different times during a summer season. The recovery data are summarized in figure 34C.

FIG. 34C.—Mosquito dispersion (data from Clark).



Recovery of a mosquito at 16 miles from the release point was the maximum distance of recovery. Relatively more recoveries were enumerated at distances nearer the source. Close agreement of the curve with the observed values suggests that extensive releases and equally extensive efforts were made to recover the released insects. Clark (1937) also developed and used the dispersion rate to calculate at what distance from human population centers must be controlled to afford given relief from the pests.

In a later publication Clark (1943) reported "... that the males of *Aedes vexans* and *Culex pipens* fly as far as the females." He found, furthermore, that the flight range of the two species was essentially the same, that one species dispersed practically as far and at the same rate as the other.

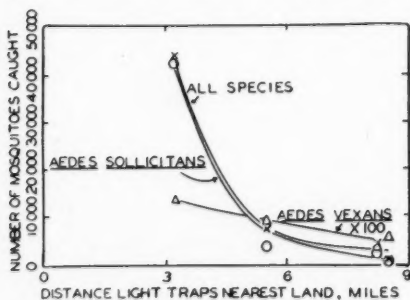


FIG. 34D.—Dispersion of mosquitoes (data from MacCreary and Stearns).

Light traps on buoys in Delaware Bay caught mosquitoes at different distances from land as reported by MacCreary and Stearns (1937). These traps were in the Bay with land at varying distances about them. They are subject, therefore, to mosquito convergence from a number of sources. The data are results of the collections for the entire summer season. The distance of each trap from the nearest land was used for the distance to draw the curves. Three curves were drawn, one for each of total number of mosquitoes (all species), *Aedes vexans* Meig., and *A. sollicitans* (Wlk.) (fig. 34D).

The "total mosquitoes" curve is practically the same as for the species *A. sollicitans* since *A. sollicitans* comprised most of the "total number." The curve for *A. vexans* is seen with a more gentle slope than that for "total mosquitoes" and *A. sollicitans*. This suggests that greater distances may be covered in the dispersion of *A. vexans* than *A. sollicitans*.

Records by MacCreary and Stearns (1937) on ratios of male to female mosquitoes caught at light traps show that as the distance from land increased the percentages of males increased. These data are given in table 2, based on total mosquitoes of all species.

TABLE 2.—Percentages of male mosquitoes at distances from the nearest land (data from MacCreary and Stearns, 1937).

Distance from land, miles	3.2	5.5	8.2	8.4
Percentage of males	0.9	1.1	3.5	6.6

These figures are suggestive of a sex-differential with reference to distance dispersion by which males disperse more distantly than females. This is, however, contrary to the usually considered behavior of mosquito sexes, and to the findings of Russell et al. (1945).

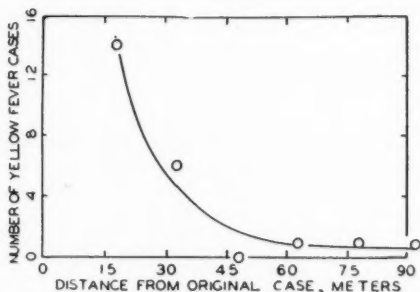


FIG. 35A.—Incidence of urban yellow fever (data from Walcott et al.).

An epidemic of urban yellow fever, a disease transmitted by mosquitoes, was shown by Walcott et al. (1937) to be localized about an original case. The distance range given was conveniently divided into classes having 15 meter intervals, which with the number of yellow fever cases in each class were used for drawing a curve (fig. 35A).

A rapid rate of disease decrease with distance increase from the original case was found. A low incidence rate was reached at 62.5 meters from the

original case, where by curve values $1/23$ as much disease could be expected as at 17.5 meters. An incidence of zero cases of disease was apparently reached at some more remote distance than 100 meters.

Casey and Brown (1938) found encephalitis epidemics, generally attributed to spread by insects, centered near settlements where lack of outdoor sanitation, open sewers, ponds, streams, garbage and tin can dumps, and other features of its epidemiology existed. They reported, "All foci of encephalitis were situated within a mile, and all except 1 within $1/2$ mile of the small stream . . .," conditions common to certain mosquito borne diseases.

Simuliidae.—In connection with studies of onchocerciasis disease McMahon (1940) gave data on dispersion of the vector, *Simulium*. Different fly densities were recognized, and some dispersion data were given. The number of specimens, all *Simulium neavei* except one, caught at contiguous distances from the river are tabulated as follows:

Fly density	Distances			
	On river bank	100 yds.	200 yds.	300 yds.
31	5	6	9	1
41-31	—	37	45	18

These data indicate *Simulium* dispersion to distances of at least 300 yards, although the rate of dispersion is not well defined, neither is a figure given to illustrate the effects of distance. The data indicate that distances greater than 300 yards are required to cover the distance of *Simulium* dispersion. Denser initial fly populations would alter somewhat the distances to which low levels of fly populations would expand.

Tabanidae.—A dearth of published records on horsefly dispersion was reported by MacCreary (1940) in his studies of the Tabanidae. Male horseflies were generally believed, however, to disperse rather restrictively near their origin. In the course of trapping mosquitoes, details of which were given by MacCreary and Stearns (1937), some records of horsefly dispersion became available. The following circumstances regarding the collections, although they do not detract from the value of the results are given for consideration: (1) the light traps were located on lighthouses near the middle of Delaware Bay, (2) the distances are those to the nearest land, (3) the horsefly source must have been in many instances more remote than the nearest land, (4) the insects were attracted to the mosquito light traps, and (5) they represent a season's collection, ranging from 31 to 98 nights operated, per trap. There is an irregular rate of horsefly decrease with distance increase. A tabular arrangement is used, therefore, for presenting the results in which three genera containing ten species are given as total insects collected (table 3).

TABLE 3.—*Tabanidae* collected by mosquito light traps on lighthouses in Delaware Bay at distances from the nearest land (Data from MacCreary, 1940).

Horseflies	Miles from nearest land			
	3.2	5.5	8.2	8.4
Males	80	89	4	0
Females	82	135	7	15
Total	162	224	11	15

These data suggest a rapid rate of decrease of horseflies with increase of distance to near 8 miles at which low levels of the insects are present. Horsefly dispersion is seen to exist in terms of miles, for both males and females, and for several species.

Cecidiomyiidae.—Hessian fly, *Phytophaga destructor* (Say), infestations were found by Jones (1937) to be more intense in wheat fields nearer swales than at more remote distances. The midclasses of the distance intervals and the percentages on infestations were used for drawing a curve (fig. 35B).

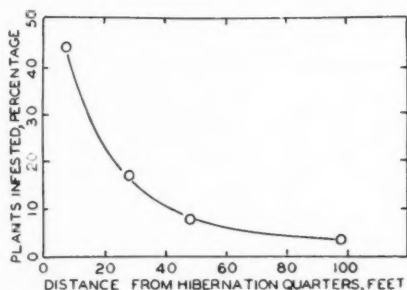


FIG. 35B.—Concentrations of Hessian fly infestations (data from Jones).

The principal infestations, those of most economic severity, were located nearer the swales, in the vicinity of hibernation quarters. Flattening of the curve began at near 80 to 100 feet from the swales to assume a low level of infestations.

In a reference frequently cited in dispersion literature McCulloch (1917) reported on the number of hessian flies caught by screen traps at distances from wheat fields. A curve was drawn from data given (fig. 35C).

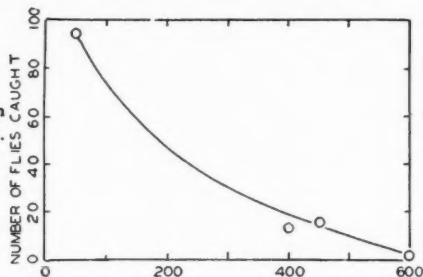
About one per cent as many flies were taken at 600 as at 100 feet from the wheat fields, showing a rapid rate of regression for the hessian flies. The agreement of the observed with the curve values is considered fair.

Syrphidae.—Dispersion of the female narcissus bulb fly, *Merodon equestris*

(F.), from the feeding habit to narcissus plantings for egg deposition is manifest by the resultant progeny. Doucette et al. (1942) gave data in appraisal of this dispersion activity, from which a curve was drawn (fig. 35D).

The marginal influence is over four-fold greater, by curve values, at 7 than at 300 yards. Infestations in smaller plantings, therefore, would show less mar-

FIG. 35C.—Dispersion of Hessian flies (data from McCullough).



ginal influences. An aid in control suggested by the marginal influence is the removal of plants on which the adults feed. The distance suggested is 300 yards or more from about the bulb plantings.

Calliphoridae.—Extensive data were given on dispersion of a fleece worm, *Phormia regina* (Meig.), and the secondary screwworm, *Cochliomyia macellaria* (F.) by Bishopp and Laake (1921). Flies were marked and liberated

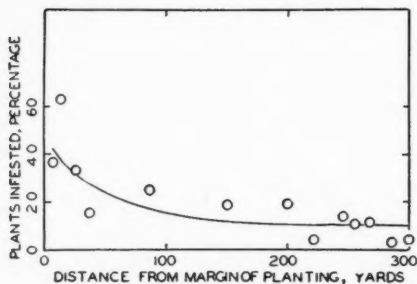


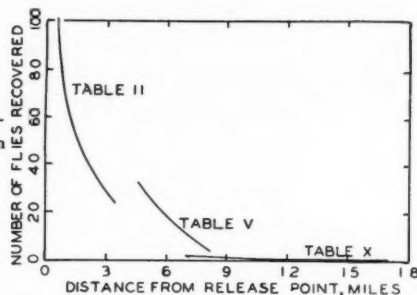
FIG. 35D.—Incidence of infestation of the narcissus bulb fly (data from Doucette et al.).

after which part of the liberated flies were recovered at different distances in each of the four cardinal compass directions from the release point. Results were given of three experiments in which the distances from the release to the recovery points ranged from 0.4 to 3.5, 4.1 to 8.2, and 7.0 to 17.8 miles, respectively. Statistical analyses showed that the differences were attributable to factors other than compass directions. The data from the different directions were, therefore, combined for each distance range, and for each species. The curve for *C. macellaria* is given in figure 36A.

The regression curves for each of the distance groups are expressive of

dispersion to several miles from the release point. Low levels of fly recoveries existed, however, at about 8 to 10 miles from the release points. The three curves have somewhat similar contours which indicates that the data were sufficient to show the dispersion rates.

FIG. 36A.—Dispersion of *Cochliomyia macellaria* (data from Bishopp and Laake).



The greater numbers of flies liberated for the intermediate distance range, 4.1 to 8.2 miles, obviously account for the greater number recovered, in comparison with the other two distance ranges. The observed values were not plotted in the figure in order to illustrate the curve slopes.

Dispersion of primary screwworm, *Cochliomyia americana* C. & P., larvae was shown by Travis, Knipling, and Brody (1940) to be localized about animal carcasses. Conversion of the data were made to the number of larvae per square foot, and of the diameters to radial distances for drawing the regression curve of larval dispersion (fig. 36B).

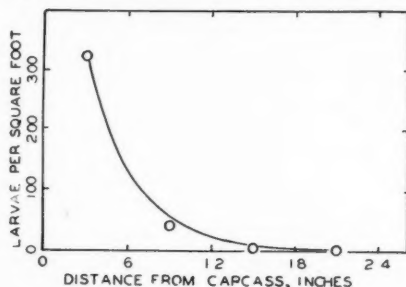


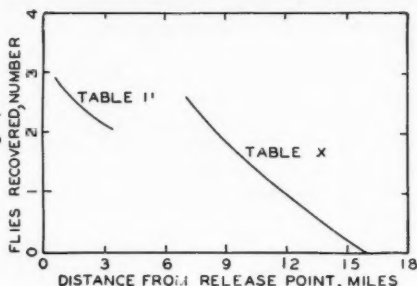
FIG. 36B.—Dispersion of primary screwworm larvae (data from Travis et al.).

Primary screwworm larvae were found to disperse restrictively, a few feet from their origin. The short distance of larval dispersion was evidence for experimental work on soil treatment in the practise of localized control during the larval and pupal stage of the insect. It would appear that the total distance-dispersion of this species could be utilized in its control during the immature stages by soil disinfestation about host animal carcasses.

Releases of *Phormia regina* (Meig.) and later recovery of some of them reported by Bishopp and Laake (1921) were in two distance ranges, 0.4 to 3.5

and 7.0 to 17.8 miles. The data without reference to compass direction, from each of the two distance ranges were used for drawing two curves (fig. 36C).

FIG. 36C.—Dispersion of *Phormia regina* (data from Bishopp and Laake).



A slight slope of the regression curve is shown for the 0.4 to 3.5 mile distance range. The curve numbers of flies are 2.90 and 2.03 at 0.4 and 3.5 miles, respectively. The computed number of flies at 7.0 miles was 2.58, while at 16.0 miles in the 7.0 to 17.8 mile distance range 0 flies was calculated to have been reached. The detailed observed values were omitted in order to show the curves and the rates of slope. Distant or widespread dispersion of the black blow-fly appears to occur over many miles.

Muscidae.—Three papers presenting dispersion data on the housefly, *Musca domestica* L., were used, namely those by Bishopp and Laake (1921), Hodge (1913), and Parker (1916).

The data given by Bishopp and Laake (1921) in three experiments were determined to show no significant directional influence. They were, therefore, justifiably combined without further regard for compass direction for each experiment (fig. 36D).

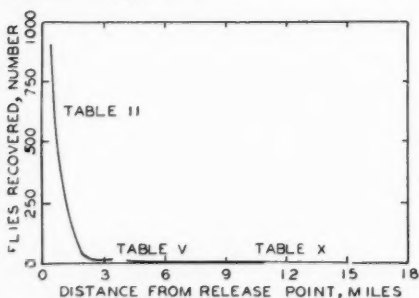


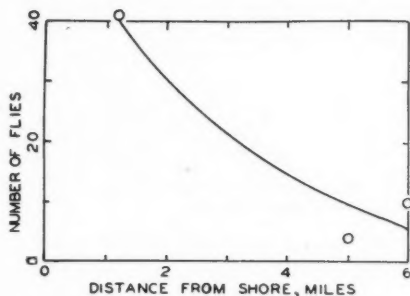
FIG. 36D.—Dispersion of houseflies (data from Bishopp and Laake).

There is a very rapid decrease at distances nearer the liberation points, followed by less rapid decreases at more remote points. The curve for the 7.0 to 17.8 mile distance experiment reaches zero at near 15 miles although the maximum recovery was at 13.14 miles. The similarity of contours of the three regression curves makes them more reliable.

The data given by Hodge (1913) included houseflies, stable flies, and blue bottle flies. The distances off shore over water to the collection points were $1\frac{1}{4}$, 5, and 6 miles. The reported number of flies for each of the respective distances is as follows: houseflies 41, 4, and 10; stable flies 9, 25, and 22; blue bottle flies 4, 12, and 1. A curve was drawn from the housefly data (fig. 37A).

More distant dispersion of flies is shown by the data from this reference than by the data from Bishopp and Laake (1921) and by Parker (1916). The numbers of flies of the different kinds do not show a well defined rate of decrease with distance increase. The value of this reference regarding its quantitative contribution may, therefore, be questioned.

FIG. 37A.—Dispersion of houseflies (data from Hodge).



The data by Parker (1916) on the housefly are very detailed. From the list of data the average number of houseflies caught per trap-day (the time a trap was in operation at a given location) for each distance class was figured. The distance range from release to recovery points was divided into nine distance classes, each of 300 yard intervals. With these data reduced from the mass of unorganized details a curve was drawn (fig. 37B).

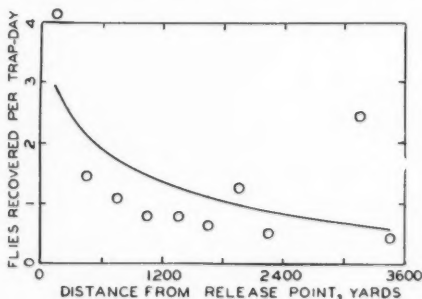


FIG. 37B.—Dispersion of houseflies (data from Parker).

Except for two distance classes, midclass points of 1950 and 3150 yards, a comparatively smooth array of observations was obtained. Closer agreement of observed and curve values is lacking because of these two variants. Recovery of some flies was made at practically two miles from the release point. Disper-

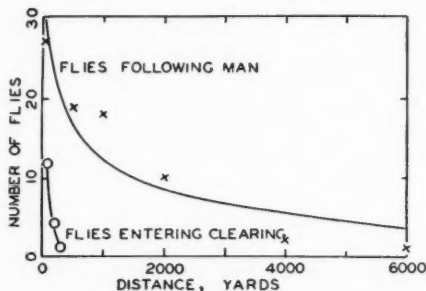
sion did not end at two miles, however, but continued in some degree to more remote and unknown distances.

Data on tsetse fly, *Glossina morsitans* Wst., dispersion activity in search of host animals were given by Swynnerton (1936). In one set of data flies entered a clearing from fly bush in search of their target. The three distance classes with the number of flies in each class were used for drawing a curve (fig. 37C).

Comparatively short distances were traversed by flies in a clearing to strike their target. Detection and attack of the target decreased rapidly as the distance from the fly habit increased.

In another set of experiments Swynnerton (1936) showed that tsetse flies penetrated Itigi-type thicket following man, and also showed how far they followed him. A curve was drawn to show the rate of fly decrease with distance increase for this activity (fig. 37C).

FIG. 37C.—Incidence of tsetse fly attacks (data from Swynnerton).



Most flies failed to go 2000 yards. Distances to, and including 6000 yards, however, were shown to have been covered by some of the flies following the host. Agreement of the observed and curve values is fair and indicates the trend of these fly activities.

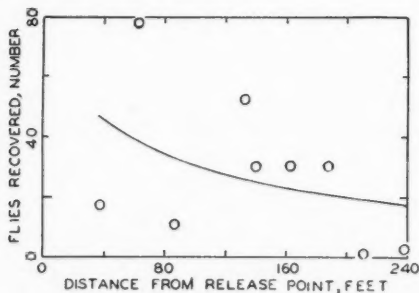


FIG. 37D.—Apple maggot fly dispersion (data from Phipps and Dirks).

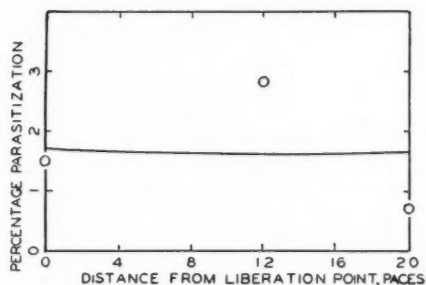
Trypetidae.—A dispersion study was made by Phipps and Dirks (1932) on the apple maggot fly, *Rhagoletis pomonella* (Walsh), in which flies were marked and liberated. Some of them, 11.8 per cent, were later recovered at different distances from the release point (fig. 37D).

An indication of the dispersion rate of marked apple maggot flies is shown to occur to over 200 feet. Close agreement of the curve with the observed values is lacking. Directional effects were found by the authors in which dispersion was in northeasterly or southeasterly directions. The presence of host plants may have affected these directional results.

Six families of Hymenoptera are represented in this review of the literature from which dispersion data were taken. In all cases the data concerned economic species, principally parasites.

Ichneumonidae.—A very limited study on parasitization of the wheat stem sawfly, *Cephus cinctor* Nort., by the parasite *Collyria calcitrator* Grav. as affected by the distance of dispersion was reported by Smith (1931). Two fields, each with three distances and percentage of parasitization data at each distance were given. The data from the two fields were combined in order to draw a curve (fig. 38A).

FIG. 38A.—Incidence of parasitization of the wheat stem sawfly (data from Smith).



A very slight sloping curve is the result. This slight slope may be the result of (1) too limited distances involved in determining the dispersion, or (2) too limited observations which resulted in wide variations in the observed parasitization. Twenty paces showed little difference effect of distance.

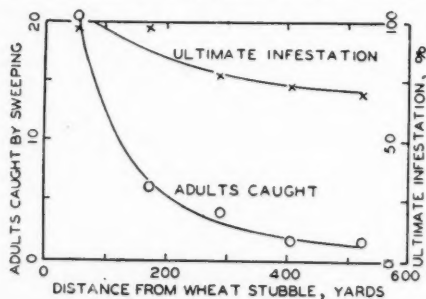
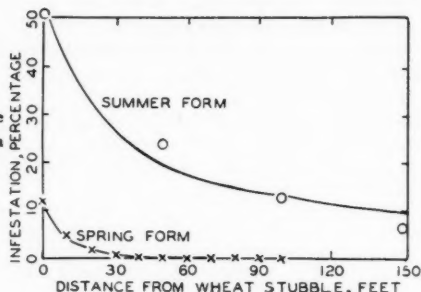


FIG. 38B.—Dispersion of the wheat jointworm (data from Chamberlain).

Eurytomidae.—Dispersion of the wheat jointworm, *Harmolita tritici* (Fitch), was found by Chamberlain (1941) to have a relationship with the distance from wheat stubble. Data from two methods of sampling the field infestations were

given, (1) sweeping the plants for specimens soon after spring emergence, and (2) determining the percentages of post harvest infestations. In each of five distance classes the average number of adults per 10 strokes of a net from the data given for the west side of the field, and the average per cent of ultimate infestation for the field were data used for drawing regression curves (fig. 38B).

FIG. 38C.—Dispersion of the wheat strawworm (data from Larrimer and Ford).



At a distance of 500 yards from wheat stubble the number of adults per 10 sweeps reached low proportions compared with nearer distances. The curve values at 58 and 522 yards were 20.3 and 1.3, respectively. Post harvest examinations showed, by curve values, that infestations of 100 per cent existed up to 80 feet from wheat stubble, and that an infestation measuring 72 per cent existed at 522 yards, the maximum distance under observation.

Another dispersion study on the wheat strawworm, *Harmolita grandis* (Rly.) form *minutum* (Rly.), was reported by Larrimer and Ford (1919). Data on the spring and summer forms were given. Since the spring form

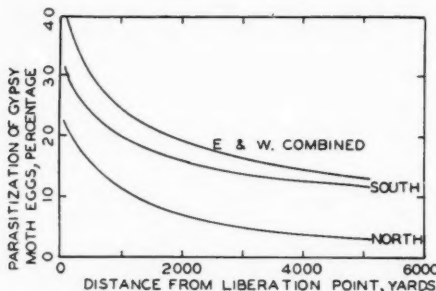


FIG. 38D.—Dispersion of a gypsy moth egg parasite (data from Crossman).

is wingless and the summer form is winged we may expect differences in the rates of dispersion. Curves representing dispersion of each of the spring and summer forms, each summarized from observations in eight fields, are given in figure 38C.

An obvious difference between the forms is the heavier infestation by the

summer form. Another difference is in the slope of the curves in which a less rapid rate of declination existed for the winged than for the wingless form. This indicates more equalization of the winged summer form over a greater distance from the source, more distant dispersion. A common similarity of the curves is the heavier infestation of each near the stubble where the insect hibernates.

Eupelmidae.—The hymenopteron *Anastatus bifasciatus* Fonsc., a parasite of gypsy moth eggs, was shown by Crossman (1917) to disperse from the liberation point to more than a mile. Data on the parasitization of gypsy moth eggs, at different distances along compass lines intersecting at the liberation point of a parasite colony, were presented by Crossman (1917). Data taken from the figure showed that the parasitizations were so similar in the east and west directions that they could be justifiably combined for one curve, and that the data in the north and the south of the liberation point were so dissimilar in amounts of parasite distribution that separate curves should be drawn from them. These three curves are given in figure 38D.

A low level of parasitization was reached at nearly a mile from the liberation point. Most parasites were in the east and west, and fewest in the north, illustrative of directional influences. The three curves have similar contours showing that the rates of dispersion were practically equal in all directions from the liberation point.

Trichogrammatidae.—In view of the colonization, liberation, and other studies on the parasite *Trichogramma minutum* Rly. reported so far one might expect that some dispersion constant had been determined for the species. Three papers, however, with data given in an organized form were located from which two curves were drawn.

Dispersion data given by Bare (1935) measured parasitization resulting from liberations of the egg parasite in celery fields. These data cover relatively short distances. The observed values are presented in tabular form as follows:

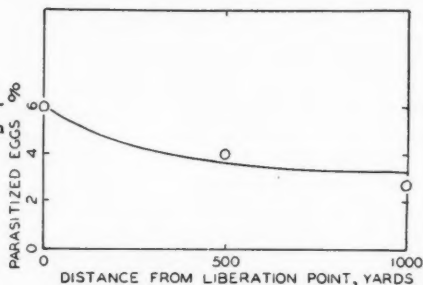
Parasitization (percent)	Distance from liberation point (feet)							
	0	2.5	5.0	7.5	10.0	12.5	18.0	100.0
Table 2.....	28.57	32.60	63.60	18.75	54.14
Table 4.....	59.70	42.10	7.93	20.24	62.50

As may be noted, neither trend nor rate of dispersion are indicated. A curve determined from the data in table 2 actually showed an increase in parasitization with an increase in distance. In table 4 the data were taken over a distance range of from 0 to 12.5 feet, a very short distance to show dispersion of organisms except those having very short dispersive powers. Owing to the wide variations in the observations and lack of dispersion trend no curve is drawn for this publication.

Dispersion rates of *Trichogramma minutum* Rly. were reported by Hinds et al. (1933) to be measurable in terms of hundreds of yards. They showed also that parasitized sugar cane moth borer eggs were first parasitized nearest the release point, and that they were later found 500 and then 1000 yards distant. The rate of reduction with distance increase is shown in figure 39A.

Distances of 500 and 1000 yards affected the percentages of eggs parasitized. The rate of reduction is considered slight, indicating that dispersion continued to some distance exceeding 1000 yards.

FIG. 39A.—Dispersion of *Trichogramma minutum* (data from Hinds).



The data on *Trichogramma minutum* Rly. dispersion by Schread (1932) from the four directions were combined and averaged for each distance class, in a parasitization study of the oriental peach moth. The averages were used in drawing a curve to indicate the dispersion trend of these data (fig. 39B).

Within the comparatively short distance range under observation, 18 to 90 feet, the expected percentages of parasitization were 61.6 and 38.6 for the respective distances. Satisfactory dispersion was reported up to 90 feet from the liberation point. This comparatively short distance range was centered near the 50 per cent parasitization level.

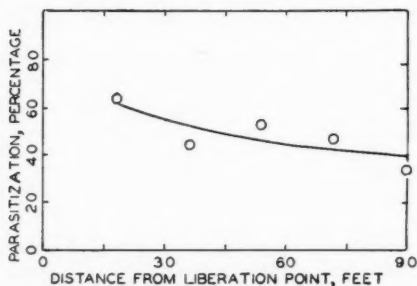
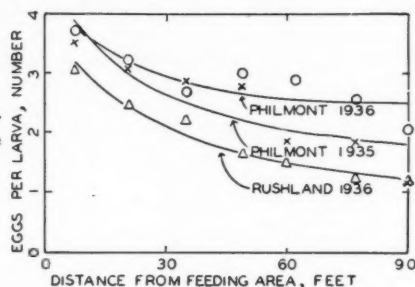


FIG. 39B.—Dispersion of *Trichogramma minutum* (data from Schread).

Tiphiidae.—*Tiphia vernalis* Rohw., a parasite of Japanese beetle larvae, was found to deposit more eggs near the feeding place of the *Tiphia* adults. Superparasitization data were given by Gardner (1938) from one location for two years and from another location for one year. A test showed that the data

differed considerably by years and by locations which justified drawing a curve for each year and each location (fig. 39C).

FIG. 39C.—Incidence of superparasitization of Japanese beetle larvae (data from Gardner).



Superparasitization was shown to occur at distances up to 100 feet from the area where adults were feeding. An important consideration in the evaluation of the effectiveness of a parasite is thus illustrated and emphasizes the need for information on the dispersion habits of parasites. The three curves are somewhat similar in curvature indicating similar effects of distance although different levels of superparasitization occurred in different locations and different years.

Apidae.—The member of this family represented by dispersion data is the honeybee, *Apis mellifica* L. Honeybees have two principal dispersion activities, (1) the distance swarms disperse from the parent colony before a permanent abode is reached, and (2) the distances to which honeybees go for the collection of nectar, pollen, water, and propolis. The distance swarms disperse in the sense of dispersion for reproduction of the species may be called the true dispersion of the honeybee. No data are known which would show the regression of this activity. Some worthwhile contributions to the knowledge of the

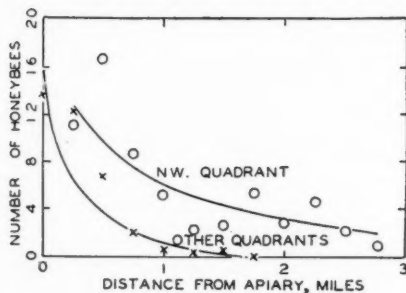


FIG. 39D.—Distribution of honeybees about an apiary (data from Eckert).

distance honeybees disperse for the collection of colony needs, however, have been made. The distances to which bees go for the collection of nectar was termed "flight range" by Echert (1933). This term appears descriptive since it is necessary for honeybees gathering nectar and other colony needs to return

to the permanent abode whether the method of movement is active or passive.

The publication by Eckert (1933) has reference to the collection of nectar for the production of honey. Eckert (1933) reported the number of honeybees observed at different distances from the apiary and in the four directional quadrants. A greater number of bees was shown to be in the northwestern quadrant. The data from the northeastern, southeastern, and southwestern quadrants were so similar as to be justifiably combined for a curve. Two curves, therefore, are shown (fig. 39D).

Similar curvilinearities of the two curves are observed. At 0.25 mile from the apiary the number of honeybees, by the curve values, are 12.8 and 6.1 for the northwestern and combined quadrants, respectively. At 1.50 miles from the apiary the expected numbers of honeybees were 4.6 and 0.3 for the northwestern, and combined quadrants, respectively. Distances at which no honeybees might be expected are greater than 2.75 miles for the northwestern, and near 1.75 miles for the combined quadrants. It was found, however, that bees flew distances up to 8.5 miles to areas where much nectar was being secreted.

The numbers of honeybees are thus shown to be distributed around an apiary by the radial distance relationship,

$$\text{Expected number of bees} = a + b (\log \text{ of distance}).$$

The gain in weight of honeybee colonies was shown by Eckert (1933) to approximate a straight line trend or relationship by plotting the data on regular uniform graph paper. It is portrayed by the regular regression formula,

$$\text{Expected number of bees} = a + b (\text{distance}).$$

Considerable work of a qualitative nature on pollination of fruit trees has been reported. These reports often show that one or several factors, without evaluation of their importance, are effective pollinating agents. The honeybee, an agent of pollination of many plants, is credited with pollen distribution at distances from the location of honeybee colonies by some published data. Since pollen is also dispersed by agents other than honeybees references are also presented under the respective headings of the given units.

Hutson (1926) made a rather extensive study of honeybees in relation to apple pollination. This work appears to be the source of the often recommended, "one honeybee colony per acre of fruit," for apple pollination. This may be an approximate number, but the most effective number would vary considerably, depending on the conditions involved.

A comparison of 5- and 12-colony groups was given by Hutson (1926) through enumerating the number of honeybees working at blossoms at different distances from each of the separate groups. Although the counts of honeybees varied somewhat on different days there was no significant difference attributable to compass direction with either 5- or 12-colony group. Distances provided significant differences with the 12-colony group, but insignificant differences with the 5-colony group. Two curves were drawn, one for each of the 5- and 12-colony groups, all counting dates combined (fig. 40A).

With the 12-colony group a four-fold distance increase, from 25 to 100 yards, gave an approximate five-fold decrease, 33.0 to 6.5 (based on curve

values), in the honeybee population density change. A slight but perceptible increase in the number of honeybees was found with distance increase in the 5-colony group. This slight increase combined with the insignificance of the distance groups indicates that the 5-colony group made no contribution to the honeybee population level in nearby trees although it may have contributed to the general population level of the entire orchard.

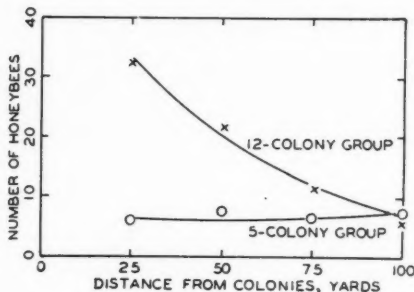


FIG. 40A.—Dispersion of honeybees (data from Hutsoin).

The wide differences between the curves of the 5- and 12-colony groups (fig. 40A) at distances up to nearly 100 yards from the group locations illustrate the effects of denser population at the source. At nearly 100 yards from the colony groups, where the curves intersect, a general orchard population density of honeybees appears to be in evidence. At this distance and beyond, the 12-colony group appears to have lost its effectiveness in increasing the honeybee population.

Original data given by Hutson (1926), with distance expressed in terms of tree spaces and average number of honeybees observed per tree, illustrate how the number of honeybees was reduced by distance increase from the colony. The curve was drawn with distance in terms of tree spaces and the average of honeybees per tree, where two trees were equidistant from the colony, otherwise from one tree (fig. 40B).

The observed number of honeybees per tree remained the same up to 10

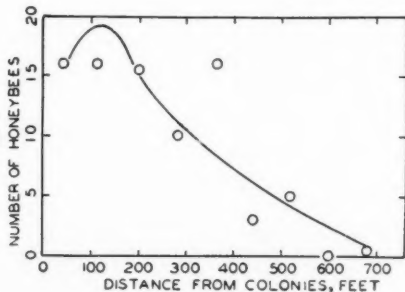


FIG. 40B.—Dispersion of honeybees into an apple orchard (data from Hutson).

tree spaces (200 feet) distance. The curve indicates, however, that reduction began at about 5 tree spaces (100 feet). The number of honeybees per tree became less with distance increase until zero bees was approached at nearly 35 tree spaces (700 feet) from the colony.

An experiment on spacing of colonies in an orchard was reported by Hutson (1926) in which a colony of bees was placed after every tenth tree (200 feet apart). The results were summarized by Hutson (1926) in which, "The counts of bees working flowers in an orchard with hives placed every 200 feet each way showed little variation."

Another experiment was reported by Hutson (1926) in which counts were made of honeybees visiting bouquets of pollinator blossoms at nearby distances from the colonies. Although three varieties of apples were tested and data were taken on two different days all data were summarized in distance groups for drafting a curve (fig. 40C).

Markedly fewer honeybees visited the bouquets at less than 10 feet than at more remote distances. These data are in agreement with the belief generally held by experienced apiarists that honeybees pass flowers near (within a few feet) the colony and work on those that are farther away.

Honeybee dispersion to pear blossoms for pollen gathering reported by Vansell (1942) included data on number of blossom visitors at distances from the colonies. A curve was drawn from data obtained during observations over a three year period (fig. 40D).

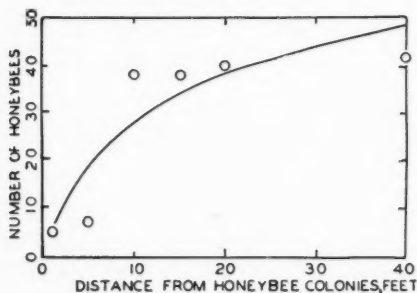


FIG. 40C.—Visitations of honeybees to bouquet blossoms (data from Hutson).

A distance of 560 feet reduced the number of honeybee visitors to nearly one-fifth as many at 60 feet. Considerable dispersion to distances greater than 600 feet appears evident. Blossoms near the colonies, shown by Hutson (1926) (fig. 40C) to be visited less frequently than those at slightly greater distances, may have influenced the observed value at the nearest trees and consequently the curve slope.

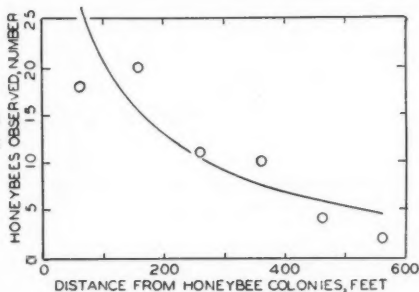
Honeybees gathering pollen were believed by Vansell (1942) to secure pollen within a short distance of the colony site, while honeybees gathering nectar, another activity, were obliged to fly a greater distance to obtain sufficient nectar. Two rates of dispersion, therefore, may be observed for honeybees, depending on whether they are gathering nectar or pollen. The need of

or the availability of the colony may be the governing factor in the rates of dispersion.

Vertical Dispersion

Considerable and valuable data have been reported on collection of organisms at different elevations above ground level. These data show that many bacteria, pollen, seeds, insects, and arachnids have high vertical dispersions. It is generally accepted that widespread horizontal dispersion must result from organisms drifting to earth from once attained high altitudes. Some relationship undoubtedly exists between high vertical dispersion and widespread hori-

FIG. 40D.—Honeybee dispersion to pear blossoms in pollination data from Vansékl).



zontal dispersion. The form and amount of any relationship between the two types of dispersion, however, have not been shown, nor is it considered safe to presume that distant horizontal dispersion follows high vertical dispersion.

Vertical distances or strata of air, soil, water, or of other media are essential for use by organisms in dispersing horizontally. Distances undoubtedly vary with species and conditions in order to cover the extremely wide ranges that are possible. It is of interest to present instances of vertical dispersion to compare with those that are horizontal.

Vertical dispersion studies with quantitative data given have been published by several workers. These publications are similar in showing that most organisms are collected nearer the ground surface. The publications on vertical dispersion are much less abundant than on horizontal dispersion. These references are listed in order of lower to higher forms of organisms as for Horizontal Dispersion, under the convenient headings of Microorganisms and Insects.

MICROORGANISMS

Bacteria.—In reporting microbiological studies of the upper air Proctor (1934) collected bacteria up to 15,000 feet. The rate of bacteria decrease with elevation increase is shown in figure 41A. About $1/22$ as many bacteria were found at 1,500 as at 15,000 feet. Should the curve continue at the same rate from 1,500 to 0 feet as between 15,000 and 1,500 feet 450 bacteria could be expected.

Two curves were drawn from data given by MacQuiddy (1935) from the different collections (fig. 41B). These curves are somewhat different. One indicates that many more bacteria existed at lower than at higher elevations, whereas the other (fig. 41B, table 2) indicates little change with increase in altitude. Different conditions doubtless affected the bacterial contents of the air sampled. Variations in the samples obtained, however, may account for part of the differences.

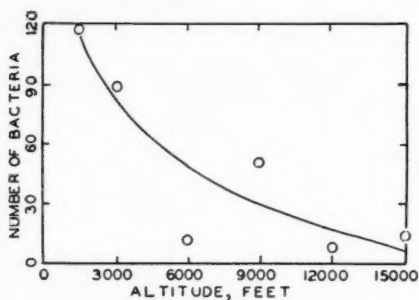
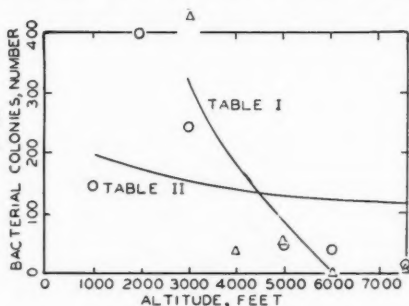


FIG. 41A.—Vertical dispersion of bacteria (data from Proctor).

A report of vertical dispersion of bacteria was made by Mischustin (1926) of collections to over 6,000 feet. The data in this report were given in terms of the numbers of bacteria per liter of air (fig. 41C). The flattened curve resulting indicates little change in the abundance of bacteria as affected by vertical distances, in the range of observations covered. Although a rather wide divergence is seen between observed and curve values some confirmation of the

FIG. 41B.—Vertical dispersion of bacteria (data from MacQuiddy).



curve slope is seen in the curves drawn from the data by Proctor (1926) and MacQuiddy (1935). Spore forming bacteria were indicated to have dispersed to greater heights than non-spore forming kinds.

The results illustrated in the last three figures show more organisms existed nearest the ground, and they also show that despite differences in the abundance of bacteria at the different altitudes rather similar rates of curve slopes result. Curves drawn from the data of Proctor (1934) and Mischustin (1926)

are more similar to the curve with the more gentle slope from MacQuiddy's data.

A very interesting report was made by Brown (1936) on the collection of microorganisms high above an arid soil in Arizona. He found that several different genera of bacteria and fungi adhered to agar traps by two minutes exposures up to 5,700 feet above ground.

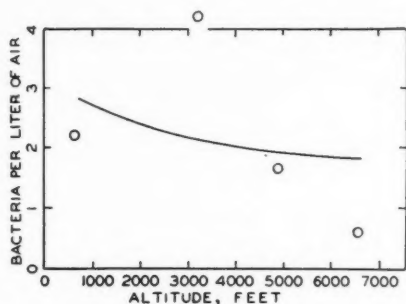


FIG. 47C.—Vertical dispersion of bacteria (data from Mischustin).

Several genera of bacteria and fungi were collected by Wolf (1943) through the exposure of ordinary nutrient agar plates at different altitudes. Graphic illustrations were used to show the number of organisms per cubic foot of air at different altitudes and on two different days. Considerable fluctuations appear to have been effected by different altitudes. Some estimated values, organisms per cubic foot of air, were taken from the graphs and are presented in tabular form as follows:

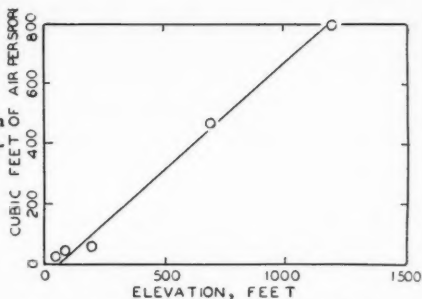
Collection date	Altitude (feet)					
	1,000	2,000	3,000	4,000	5,000	6,000
Dec. 6, 1941.....	0.68	0.23	0.18	0.03	0.02	0.02
Jan. 25, 1942.....	0.34	0.20	0.13	0.10	0.08	0.06

The collection made Dec. 6, 1941 shows that more organisms were collected nearer the ground, whereas collections made Jan. 25 show that more organisms dispersed farther vertically.

Fungi.—The number of onion mildew spores collected at different elevations above onion sets on which spores were being produced were recorded by Newhall (1938) in terms of cubic feet of air per spore. A curve was drawn from these data (fig. 41D). The most spores were collected near the ground surface with decreased numbers by altitude increase, except for the 1,500 foot

elevation. For some reason this extreme variant appears "out of line." It was excluded from the computations.

FIG. 41D.—Incidence of onion mildew spores (data from Newhall).



The incidence of azalea flower spot disease infections was found by Smith and Weiss (1942) to be greatest nearest the ground surface. The incidence curve is shown in figure 42A. Low levels of disease infections were reached at heights of 20 to 30 inches. No infection was reported above seven feet. Although part of the infections are attributable to spore dispersion more favorable conditions nearest the ground surface may account for part of the incidence rate.

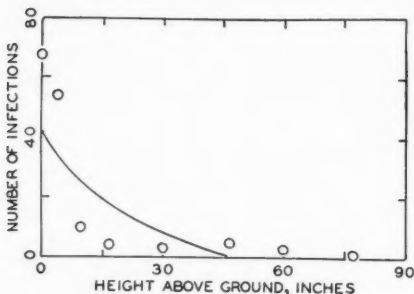
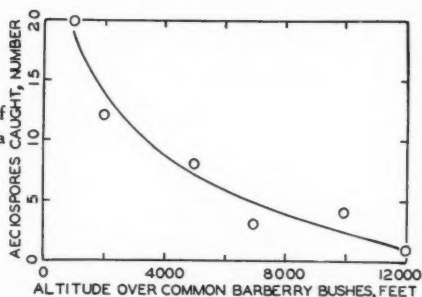


FIG. 42A.—Incidence of azalea flower spot disease (data from Smith and Weiss).

Considerable data were published by Stakman et al. (1923) on the number of wheat stem rust, *Puccinia graminis* Pers., spores caught at different altitudes. Data were taken from among a series of records on the number of aeciospores caught on slides coated with vaseline and with glycerine jelly. These may exemplify the rate of vertical dispersion rather than give a final definition of it (fig. 42B). One spore was caught at an altitude of 12,000 which compared with 20 caught at 1,000 feet illustrates the extremes of distances and spores observed in the series. Should this rate of decrease continue to zero altitude at the same rate 66 spores might be expected. This rate of decrease is considered slow compared with the rates of decrease observed with most organisms. Considerable heights appear, therefore, not to have greatly affected vertical dispersion of wheat stem rust aeciospores.

Data from the report by Peterson (1931) show that spores of cereal rust must disperse at high altitudes. A curve was drawn from these data (fig. 42C). Nearly $1/1,000$ as many spores were recorded at 14,000 feet as at 1,000 feet elevation. This indicates a much more rapid rate of decrease in the abundance

FIG. 42B.—Vertical dispersion of wheat stem rust spores (data from Stakman et al.).



of spores with altitude increase than with the data from Stakman et al. (1923). Although the modified semi-logarithmic formula was used to calculate expected numbers the double logarithmic formula appears to give expected numbers that agree more closely with the observed values.

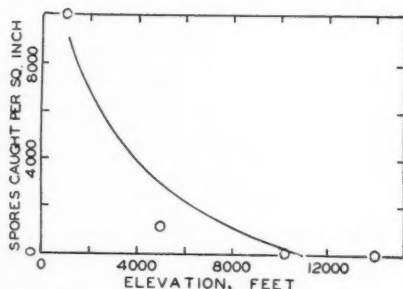


FIG. 42C.—Vertical dispersion of wheat stem rust spores (data from Peterson).

Considerable data were given by MacLachlan (1935) on dispersion of *Gymnosporangium juniperi-virginiana* Schw. and *G. globosum* Farl. at altitudes above sources of basidiospores. A curve was drawn to show the rate of spore decrease with altitude increase (fig. 42D). One minute exposure of 20 square cm. of agar plate yielded $1/125$ as many spores, based on curve values, at 1,500 as at 100 feet altitude. No spore was collected at 1,500 nor 2,000 feet.

Pollen.—From his allergy studies MacQuiddy (1935) presented data on vertical dispersion of pollen. Two rather diverse rates of pollen decrease with altitude increase are indicated from these data (fig. 43A). Low numbers of pollen counts were made at near 6,000 feet altitude. Sampling of the air occurred at two different times which may account for the different rates of

pollen decrease with altitude increase. Different atmospheric conditions apparently occurred at the different times.

The numbers of sugar beet pollen grains caught at different times were recorded by Meier and Artschwager (1938). A curve was drawn from these data, except for the 5,000 foot altitude which appears markedly out of line.

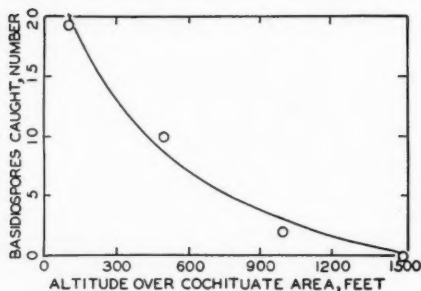
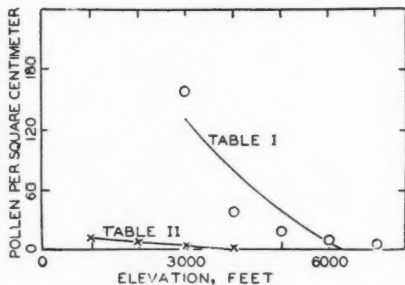


FIG. 42D.—Vertical dispersion of *Gymnosporangium juniperi-virginiana* and *G. globosum* basidiospores (data from MacLachlan).

The 5,000 foot observation, however, is plotted for comparative purposes (fig. 43B). Almost sevenfold more pollen, based on curve values, was taken at 1,000 than at 4,000 feet. Close agreement of the curve with the observed values is shown, except an apparent aberrant figure at 5,000 feet, which was according to the authors, in the "dust horizon."

FIG. 43A.—Vertical dispersion of pollen (data from MacQuiddy).



INSECTA

Freeman (1938) gave data on the composition of the aerial insect fauna at altitudes up to 300 feet. The frequencies of insect populations were given in terms of insects per million cubic feet of air, a term suggested for reporting vertical dispersions. A curve was drawn from the data given (fig. 43A). This curve with its rather gentle slope indicates 21 and 239 insects per 1,000,000 cubic feet of air at 277 and 21 feet, respectively.

The most extensive report on vertical dispersion was given by Glick (1939). Many insect species were represented by collections made at altitudes

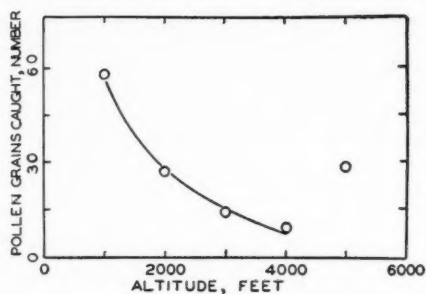
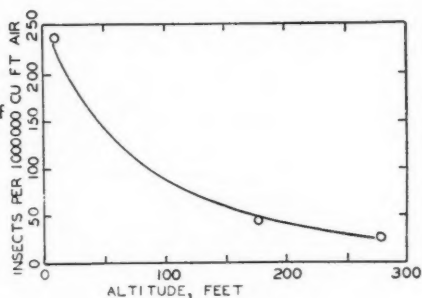


FIG. 43B.—Vertical dispersion of sugar beet pollen (data from Meier and Artschwager).

up to 16,000 feet. Several curves might be drawn from the detailed lists of species, genera, orders, or groups collected at the different elevations. One curve, representing all species, from collections taken in daylight flights, however, is used to show the number of insects per 10 minutes flying time (fig. 43D).

FIG. 43C.—Vertical abundance of insects (data from Freeman).



The average number of insects caught per unit time decreased rapidly to 1,000 feet and less rapidly thereafter. At altitudes greater than 4,000 feet few insects per 10 minutes flying time were collected as shown by variations in

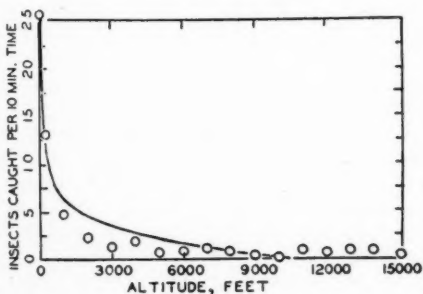


FIG. 43D.—Vertical dispersion of insects (data from Glick).

frequencies of from 8 to 80 minutes flying time required to capture an insect. Although no specimen was taken in five minutes flying time at 16,000 feet, and only one was taken in 20 minutes flying time at 15,000 feet, further sampling would undoubtedly have revealed that these altitudes were not the maximum altitude of vertical dispersion of insects. Practical difficulties, as explained by Glick (1939) prevented further collecting at the higher altitudes.

The modified semi-logarithmic formula used to compute the curve values does not provide a curve that "fits well" with these data. Neither do the data show a satisfactory curve "fit" with log-log spaced grids or any other way tried.

In studying the aerial drift of insects Hardy and Milne (1938) gave data on the number of insects collected at the different altitudes. A three-foot diameter insect net per 10 minutes flying time at different altitudes was used for sampling the air. A curve was drawn from the data given (fig. 44A).

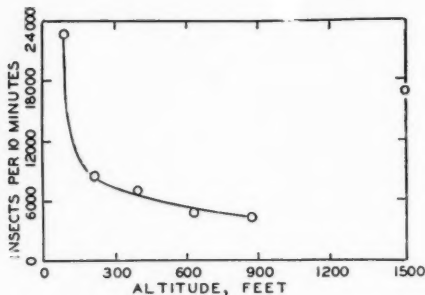


FIG. 44A.—Vertical dispersion of insects (data from Hardy and Milne).

A rapid decrease in the abundance of insects was found to about 300 feet altitude followed by a less rapid decrease. More insects were found in the lower layers of air, except at the 1,000-2,000 (midclass altitude of 1,500 feet) foot height 16,700 insects were taken which is approximately as many as at 100 feet. Fair agreement of the curve with the observed values exists. The observation at the 1,000-2,000 foot altitude was omitted from calculations for determining the curve, but is plotted in the figure for comparison.

A minor division is made in the group Insecta. The data in the above reference deal with vertical dispersion ranging from 277 to upwards of 16,000 feet. They include flights for sampling the air. The following references pertain to vertical dispersion upwards to 53 feet. Ground support, furthermore, is characteristic of the methods used in the sampling procedure.

Strips of adhesive material placed on uprights in the ground, at different heights from the ground in fields of rape, after the harvest were used by Proffitt (1939) to catch insects. Copegnaths were found more abundant at 2.7 meters height (fig. 44B). A rather slight slope of the curve upward to 2.7 meters, the maximum height of the observations, was found. Over six-fold more organisms were collected at 2.70 than at 0.17 meters.

Thysanoptera, as reported by Proffitt (1939) reached a peak of vertical

dispersion abundance at near 2 meters (fig. 44C). A sharp curvature is indicated at from 0.54 to about 2.00 meters height. The curve values at 0.54 and 5.04 meters were 667 and 1,167, respectively.

Aphid dispersion was the principal objective of study by Profft (1939). The abundance of these insects increased with height increase, up to 2.68 meters (fig. 44D). Curve values at 0.17 and 2.68 m., the lowest and highest adhesive strips under observation, were 2.1 and 19.1 aphids, respectively. A straight line function is indicated for the height range covered by these data.

FIG. 44B.—Vertical abundance of copegnaths (data from Profft).

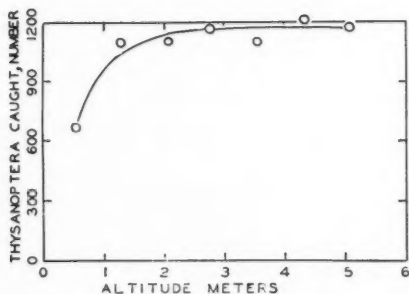
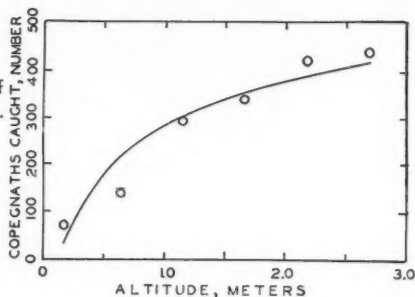
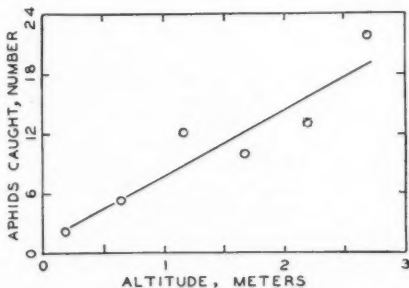


FIG. 44C.—Vertical dispersion of Thysanoptera (data from Profft).

FIG. 44D.—Vertical dispersion of aphids (data from Profft).



The regular method of least squares formula was used, therefore, to determine the curve values.

Annand et al. (1932) in studying the sugar beet leafhopper found more of these insects dispersing in the air strata nearer the ground level. A curve was drawn for the three height points given (fig. 45A). Sixty-one per cent as many leafhoppers were taken at 25 as at 8 feet. The curve has a slight slope for the given range of altitudes indicating little difference between the heights at which the insects were collected.

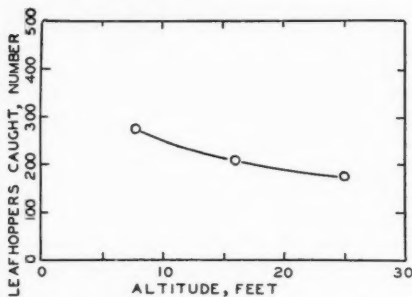


FIG. 45A.—Vertical dispersion of the sugar beet leafhopper (data from Annand et al.).

In connection with the above considerations reference is made to figures 1D and 19B, incidence of curly top disease effected by the beet leafhopper and horizontal dispersion of the insects, respectively. Long distance dispersion of the leafhoppers was found by these workers. This occurrence in connection with the vertical dispersion indicated in figure 45A is evidence for the belief that the sugar beet leafhopper may disperse distantly yet remain relatively near the ground in so doing. How many or what other organisms disperse in like manner remain for subjects of further studies.

Definitive evidence illustrative of vertical dispersion of the tobacco flea beetle, *Epitrix hirtipennis* (Melsh.) was given by Dominick (1943). Although some data were given on horizontal dispersion they are, unfortunately, not adaptable for drawing a regression curve. It was concluded from the observations on horizontal dispersion that, "There is no indication that the insects move long distances, as from county to county. These flea beetle catches sug-

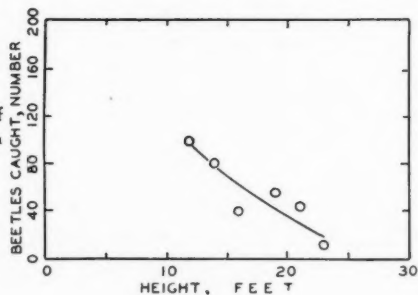


FIG. 45B.—Vertical dispersion of the tobacco flea beetle (data from Dominick).

gest that each farm produces its own flea beetles." This conclusion is in agreement with the observations by Wolfenbarger (1940) on a species of the same genus, *E. cucumeris* (Harr.). Considerable data for two different height ranges, one in classes of 1-2, 2-4, and 4-6 feet, and the other in classes of 11-13 to 22-24 feet were given. A curve was drawn from the 11-13 to 22-24 foot range (fig. 45B).

A very rapid rate of regression was found with increasing heights, from 11 to 24 feet. Less than one-fifth as many beetles were taken at 23 as at 12 feet heights, based on curve values. Some observed values lack close agreement with the smoothed curve although a satisfactory trend line is indicated.

The mean numbers of beetles taken at 1-2, 2-4, and 4-6 feet were 30, 51, and 25, respectively. Since there were 10 tables with data for this height range, all showing more beetles caught at the 2-4 foot height level than at the other two levels, the observations must be sufficient to demonstrate the beetle activity. It shows that the tobacco flea beetle disperses at 1-2 feet from the ground, but disperses more abundantly at 2-4 feet heights, and that the numbers of beetles decrease rapidly with height increase.

Vertical dispersion of coccinellids was found by Profft (1939) to be more frequent nearest the ground surface (fig. 45C). Aphids on which these beetles feed, however, were more prevalent on the adhesive strips higher above ground (fig. 44D). Expected numbers of coccinellids were 39.5 and 0.7 at 0.17 and 2.68 meters, respectively. The observed and curve values have fairly close agreement.

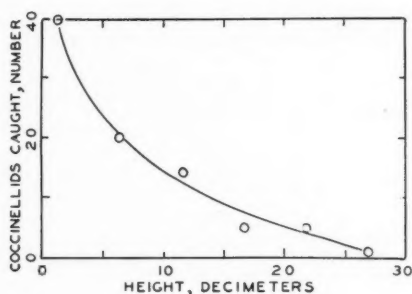


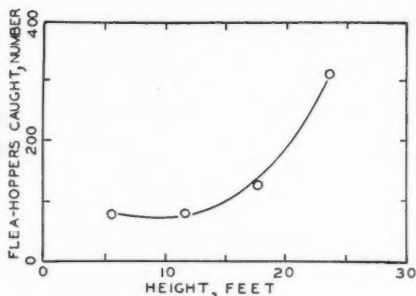
FIG. 45C.—Vertical dispersion of coccinellids (data from Profft).

These data, in connection with those given by Davidson (1925) (see figure 20D), on distance of ladybird beetle dispersion suggest that coccinellids may disperse distantly although they remain near the ground level during the process.

Vertical dispersion data were given by Gaines and Ewing (1938) on the cotton flea-hopper, *Psallus seriatus* (Reut.). Catches of these insects at distances above ground were used for drawing a regression curve (fig. 45D). Increasing numbers of flea-hoppers were caught with increased heights above ground, up to 23.5 feet the maximum height observed. A rapid rate of increase began at about 15 feet and ended at some distance above 23.5 feet.

Three of the eight specimens of *Psallus seriatus* taken by Glick (1939) at 20 feet elevation and none above 2,000 feet, in connection with the data from Gaines and Ewing (1938), suggest that the peak of flea-hopper dispersion occurs at elevations above 25 and under 2,000 feet. The abundance of insects, obviously, cannot continue to increase with increases in elevation. An interesting consideration is the elevation at which the insect abundance reaches a peak and then declines.

FIG. 45D.—Vertical dispersion of the cotton flea-hopper (data from Gaines and Ewing).



European corn borer moths were found by Ficht and Heinton (1941) to converge to light traps nearer the ground surface than to those at greater heights (fig. 46A). Almost one-third as many moths were taken by traps at 15 as at 5 feet elevations. This is an interesting observation in view of the general acceptance of the usual occurrence of more frequent infestations in taller corn plants.

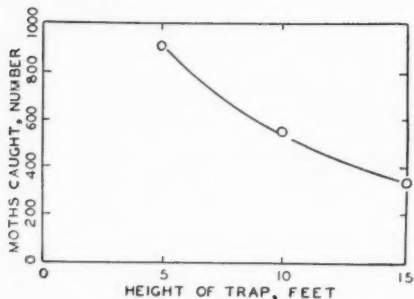
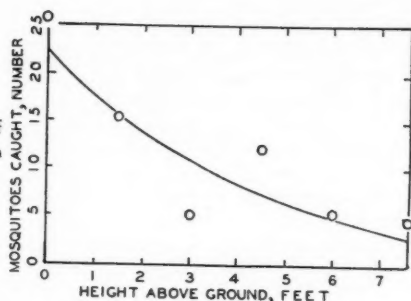


FIG. 46A.—Vertical dispersion of European corn borer moths (data from Ficht and Heinton).

The common malaria mosquito comes to rest more frequently in traps nearest the ground according to the studies by Goodwin (1942). Data were obtained from boxes used as resting places placed at different heights, up to 7.5 feet (fig. 46B). Almost eight times more mosquitoes are shown by the curve to have sought resting places at ground level than at 7.5 feet. This observation is in agreement with those of Horsfall (1942) and MacCreary (1941). Horsfall took 77 per cent of his catches at the 4 foot level and 23 per cent

at the 8 foot level. MacCreary trapped 3,166 mosquitoes of all species at 4.5 feet compared with 447 at 103 feet at one location, and 14,642 at 4.5 feet compared with 1,374 at 80 feet at another location. Since but two elevation figures with their corresponding data were given by each author for each comparison no curve is drawn.

FIG. 46B.—Vertical incidence of the malarial mosquito (data from Goodwin).



Frit flies, *Oscinella (Ocinis) frit* L., were reportedly taken at various heights by Riggert (1931) on adhesive coated screens at heights up to 60 feet. A peak of abundance was reached at near 16 feet, then the numbers declined although the insects were still plentiful between 33 and 60 feet. Körting (1931), who also trapped insects using adhesive coated parchment paper, was in slight disagreement with Riggert (1931) and reported that frit flies dispersed more abundantly nearest the ground and decreased in numbers with height increase. He reported, however, that two thysanopterans, *Limothrips cerealium* Hal. and *Haplothrips aculeatus* F., preferred heights above three feet for dispersion.

The data on fruit fly dispersion given by Profft (1939) show that they were more abundant nearer the ground level (fig. 46C). The numbers of flies, by curve values, are 413 and 117 at 0.54 and 5.04 meters, respectively. A slight slope of the curve was found which agrees well with the observed values.

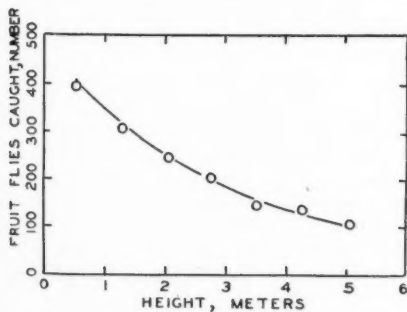


FIG. 46C.—Vertical abundance of fruit flies (data from Profft).

Part II. Generalizations

Whenever organisms become unusually abundant, especially if a sudden influx occurs, mankind asks characteristic questions, such as, Where do they come from? and How did they come? Historical evidence of discussions concerning the significance of dispersion of organisms pertain to (1) spontaneous generation, and (2) epidemics such as locust invasions, the Irish famine from potato blight, and cholera epidemics. In view of the untenable position of spontaneous generation (abiogenesis) and of the acceptance of the biogenesis concept of the origin of life it is obvious that dispersion of organisms must occur. Dispersion is a corollary of biogenesis and epidemics. Two current movements, the Interdivisional Committee on Aeriobiology of the National Research Council in America and the Insect Immigration Committee of the South-Eastern Union of Scientific Societies in England, for the collection and analysis of records of dispersing organisms indicate the contemporary significance of the subject.

Usual occurrence, trends, or habits of dispersing organism, as evidenced by dispersion and incidence studies, have suggested certain generalizations. Although categorical generalizations precluding exceptions can apparently not be formulated, certain logical deductions which appear to characterize dispersion and incidence principles are, nevertheless, presented.

Dispersions and incidences are responses of organisms in overcoming resistance of movement. Movement responses are comprehensible in terms such as distance, time, direction, and number or amount of units involved. Variations in distance, time, direction, and number or amounts, and interrelationships occur as dispersing populations react to, and move through the media surrounding the individuals. The distances dispersed are dependent on the resistance of forces between the organisms and environmental conditions.

Distance

Distances dispersed by organisms depend on the organism, species, activity, generation, or phase involved (see Part I). Many or most organisms have two or more stages, activities or phases in which different rates of dispersion are recognized. The distance ranges dispersed by the different stages, phases, or activities are often as different as different species and the rates of one cannot predict the rates of the other. Different stages of rust spores, aeciospores, uredospores, teliospores, basidiospores, and pycniospores may have different rates of dispersion for each stage. Aeciospores of white pine blister rust, *Cronartium ribicola*, for example, are generally believed to disperse in terms of miles much farther than the uredospores, which disperse in terms of hundreds of feet. Most insects disperse during the immature and the mature stages, often in terms of markedly different distance ranges.

Extremes of distance ranges, illustrated in Part I, were in terms of inches for primary screwworm larvae and European corn borer larvae, and in hundreds of miles for migratory grasshoppers, sugar beet leafhoppers, and black stem rust spores of wheat.

A factor of considerable importance, demonstrated by collections of field data and by examinations of data given by authors, is the surprisingly close agreement of data representative of dispersion by repeated observations, even if all other factors are taken into consideration. Although further evidence is needed for verification of this observation, wide differences in locations, observers, and other apparent factors frequently appear of little significance, and the rates of dispersion of an organism often seem to be remarkably consistent. This fact makes meager data more reliable and the collection of more quantitative data on the dispersion of organisms highly desirable.

Dispersion-Distance and Dispersion-Time Reciprocity.—Three examples of time elapsed and distance covered between liberation and recovery points are given [Linn (1940), Van Zwaluwenburg and Rosa (1940), and Steiner and Worthley (1941)]. The curves show that as distances from the source of the organisms increased the time required for the dispersion also increased. This is termed a positive regression. Since the number of organisms decreases with distance increase the relationship is a negative regression. Time and distance rates of decreasing organisms are shown, therefore, to have inverse relationships. The distance-time relationship has a disposition for straight-line association by semi-logarithmic conversions, as is also the association of distance and number of units illustrated in Part I.

Organisms may proceed from their origin by successive movements to the terminals of dispersion. These movements must range from an extreme of rapidly moving organisms to remotest distances, to an extreme of slowly moving organisms to the shortest distances. Actively dispersing organisms, most insects for example, may halt and proceed intermittently during the dispersion process. Passively dispersing organisms, seeds, spores, and pollen for example, may, after starting dispersion, proceed and terminate their journey without evidence of halting.

Knowledge of the distance dispersed, based on published numbers of distances dispersed as compared with those of time required for dispersion, is more useful than knowledge of the time required. The dispersion-time rate may, however, have a more important function with some organisms, for example in disease transmission or where dispersion-time might be measured more practically than dispersion-distance.

Dispersion-Distance and Dispersion-Time Differential.—In view of the reciprocity of distance dispersed and of the time spent in dispersion the discussion is extended to some comparisons of the regression rates for each of these measures of dispersion. The numbers of days spent in dispersion were changed to reciprocals in order to plot curves that slope downward. Curves were drawn, therefore, from data given in the publications by Linn (1940), figs. 18B and 18C (table 2), Steiner and Worthley (1941), fig. 23C, and Van Zwaluwenburg and Rosa (1940), fig. 25B, and are presented in figs. 47A and 47B. Smoothed curve values, determined from the respective formulae given in the Appendix, are used for plotting these curves to illustrate the features considered.

The curves illustrating dispersion-time have somewhat similar rates of slope

in fig. 47A, and less similar ones in fig. 47B. The curves in each figure illustrating dispersion-distance also have somewhat similar rates of slope. This is considered of no special significance in fig. 47A; but in fig. 47B the two curves supplement each other, since the data are considered comparable, having been recorded by the same authors, from the same general area under somewhat similar conditions and with the same species of organism.

FIG. 47A.— Dispersion - distance and dispersion-time for insects from release to recovery points [data from Linn (1940), and Steiner and Worthley (1941)]. Dotted lines are reciprocals of the dispersion-time curves; solid lines are dispersion - distance curves.

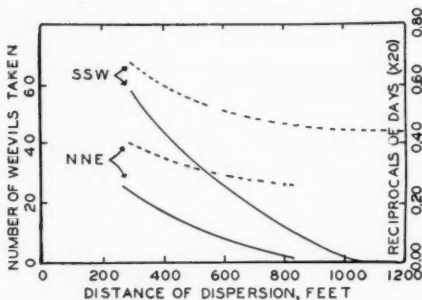
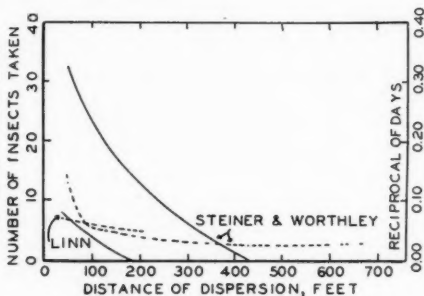


FIG. 47B.— Dispersion - distance and dispersion-time for the New Guinea sugar cane weevil from release to recovery points [data from Van Zwaluwenburg and Rosa (1940)]. SSW and NNE refer to the respective directions of dispersion; dotted lines are the reciprocals of the dispersion-time curves; solid lines are the dispersion-distance curves.

It is desirable to consider here by means of figs. 47A and 47B, how insects cease dispersion measured by two qualities, distance, and time. This is done by comparing the slopes of the dispersion-distance and dispersion-time curves, since they cover the same distance ranges. It is evident that the dispersion-distance curves are characterized by steeper slopes of decrease than the reciprocals of the dispersion-time curves. In other words, the rate of decrease in the number of insects with distance increase was more rapid than was the rate of increase in time required for dispersion. This suggests that the numbers of insects must drop off rapidly whereas those that continue to disperse must do so at a less rapid rate of movement. The full significance of this dispersion behavior characteristic, however, remains to be discussed.

The significance of the distances dispersed by genes, sperms, and ova is unquestionably considerable. Such distances, although perhaps in many or most cases they are undoubtedly of extremely short range, must be within the limits

of measurability but await future study. For data indicating the magnitude of distances traversed by these structures have not yet been recorded and further reference to their distance dispersion is, therefore, omitted.

Direction of Dispersion

Generalizations about directional effects of dispersion that are constant depend apparently on the group, phase, species or activity, or are modified by locality differences. Much evidence is indicative of omnidirectional dispersion, although there is also evidence of unquestioned unidirectional dispersion. The same species, honeybee for example, is represented by conflicting evidence indicative of inconsistency within species.

Dispersion of species of organisms that are air-borne, fungus spores of *Endothia parasitica*, *Puccinia graminis*, and *Ustilago tritici* for example, would be expected to be unidirectional in whatever direction the wind was blowing. Ört (1940) showed that loose smut of wheat dispersed in all directions, but more strongly toward the southeast. He believed that weak winds were responsible for more distant dispersion than strong winds.

White pine blister rust spores, which are wind-borne, resulted in infections of, "... comparable proportions in all directions from the central ribes," according to Buchanan and Kimmey (1938). Skewness was observed but was attributed to the presence of trees down the slope from the source of the inoculum. Data were given by Posey and Ford (1924) however, which showed that more infections occurred in the south and fewer in the eastern direction from the source of the inoculum. Reasons for these differences were not given.

Species of active disperser organisms, in which many more data on dispersion are available, fail to show uniformity with regard to directional effects. Crossman's data (1917) show directional influence of an egg parasite on the gypsy moth in which more parasite dispersion occurred in the east and west directions than in the north or south. The recent and extensive studies by Fulton and Romney (1940) on the sugar beet leafhopper show unidirectional northerly dispersions. Eckert (1933) observed more honeybees in the northwestern direction from the apiary but failed to account for this observation. Ficht, Heinton, and Fore (1940) reported with regard to European corn borer that, "... the moths normally travel against the wind ... traps in the northeast of corn fields are the first to be encountered." Van Zwaluwenburg and Rosa (1940) found that more sugar cane borers dispersed with than against the wind.

Other workers found or reported dispersions which were omnidirectional. Contrary to Eckert's data (1926) Hutson's report on honeybees showed no directional influence. Bishopp and Laake (1921) found the dispersion resultant from the liberations of thousands of flies was practically equal in four compass directions regardless of wind direction. Mosquitoes were reported by Clark (1937) to disperse in all directions. Brower (1930) believed in the case of *Catocala* that the, "movement is in no definite direction." No significant difference was assignable to directions on incidence of injuries made by the smaller European elm bark beetle by Wadley and Wolfenbarger (1944).

A tendency observed for many dispersion studies is for relatively short dispersions to be omnidirectional and for relatively long dispersions to be unidirectional. Whether this is apparent or real is a factor worthy of further study.

The simplest form of dispersion may be regarded as that in which organisms leave their origin and move outward in all directions. The more specialized dispersions, whether the action is teleological or mechanistic, is, on the contrary, that in which the dispersion is unidirectional. Organisms having a unidirectional dispersion may, by reason of greater distance covered, occupy and utilize a habitat denied omnidirectional dispersion with a shorter distance range. Unidirectional dispersion of active dispersers may be the way of least resistance, or the way of a strong attraction. Unidirectional dispersion of passive disperser organisms is along the way of the dispersing agent.

Evidence of more dispersion in more favorable directions, and of less in less favorable directions is unknown although such instances seem likely to be encountered. Those units in the more favorable directions continue and terminate their dispersion. Those units in the less favorable directions would either perish or be turned back with some likelihood that certain individuals would find their way in the more favorable directions and be an added economy to the species. Whether in an evolutionary trend survival is by chance or extends to those individuals which are capable of determining or predicting a favorable direction for dispersion, remains an unknown factor.

Factors Influencing Dispersion

Dispersion of each species of organism, phase, stage, generation, or activity usually occurs at a time in which it is in a "state of readiness." Each, therefore, may have a principal or "disperse phase." Many species, however, disperse or may be dispersed at different times during their life span. According to Uvarov (1928) the dispersion of migratory locusts is, "... induced and regulated solely by physiological factors. . . ." The "state of readiness" appears more evident from the studies of Ingold (1939) than from many biological discussions. Different external stimuli may be applied to organisms without affecting any dispersion. If these same stimuli are applied when the organism is in a "state of readiness," they apparently initiate dispersion.

Dispersion may be initiated by internal factors, such as the reproductive impulse, hunger, periodicity of habit, or gregariousness. External influential factors are overcrowding, shortage of food, change of food conditions, quantity or quality of light, temperature and moisture conditions, wind, or intervention of other organisms.

The ways of dispersion may be motivated by internal stimuli such as gregariousness, instincts or habits, and procreative stimuli. External stimuli include wind, light values, water currents, temperature and moisture gradations, available food supply and its conditions, or influences from other organisms. The influences of land elevations directly or indirectly are often sharply delimiting factors in the course of dispersion.

Termination of dispersion activities is influenced inherently by completion

of a physiological state such as mature sex development, end of reserve energy supply, fatigue, or end of hibernation or aestivation stage. External stimuli affecting termination of dispersion activities include location of favorable food conditions, wind or air currents, moisture, temperature, light, living room, and influences of other organisms. Absence of stimuli operative at the initiation and during the course of dispersion, end at or near the termination point.

Migration of Small Organisms

Most movements of small organisms are termed dispersion. These movements fit the conception of dispersion, if the organisms move away from their source but lack mass purposeful and periodical returns to their source for reproduction. There are probably exceptions to the usual procedure in which small organisms disperse to new areas, reproduce themselves, and again return, or in which they disperse to another area for a season and then return to the area of their origin for reproduction. Whether the same or new individuals return is inconsequential. With the increasing knowledge of organismal activities it may be found that really migrating species are more common and less exceptional.

Spores of the wheat stem rust, *Puccinia graminis* Pers., a passive disperser organism, migrate according to McFadden (1941). These spores are known to originate from infected wheat plants in Texas in the spring season and to initiate rust cycles on plants in distant states, as Minnesota and North Dakota. As the spores mature on wheat in the northern states, they are apparently dispersed by wind to favorable host plants, winter wheat in a moderate winter climate in Texas, where they inoculate new plants and reproduce. This is a mechanistic mode of migration of organisms, whose frequency and significance must be tested by further observations.

The spotted cucumber beetle, *Diabrotica duodecimpunctata* Fabr., may be considered migratory in view of the observations of Smith and Allen (1932). These beetles were believed to overwinter south of central Missouri in the Mississippi river valley. In the South they may be more or less active in the warmer winter climate. With the coming of summer the beetles, new adults as progeny of the beetles that moved southward and in the more northern part of the overwinter range the old adults, those which moved southward, were believed to move, i.e., migrate northward. These beetles were not known to remain in the South through the summer nor in the north during the winter.

The cotton leaf worm moth, *Alabama argillacea* Hbn., does not overwinter in the United States but disperses from the countries to the south of them. Whether populations of this moth return southward to those countries is not known. Dispersions of *Loxostege sticticalis* L. reported by Mel'nichenko (1936) in different districts in Russia may represent migrations. Several other lepidopterans are often said to be migrating. Species of the Locustidae, grasshoppers, may migrate. The destructive potato leafhopper, *Empoasca fabae* (Harr.), may be found to migrate. Until there is evidence that populations of an organism go to an area or region somewhat remote from their origin and

return, by seasonal or periodical movements, for reproductive purposes, these activities should be called dispersion.

Agencies or Means of Dispersion

Dispersion occurs largely by one principal agency or mode, and usually over a comparatively short period of time. This is necessary to (1) accomplish dispersion, (2) insure line breeding of the species, and (3) provide food and other conditions suitable for perpetuation of the species.

All organisms, on the other hand, and apparently without exception, disperse or may be dispersed by more than one agency. Furthermore, many organisms are adapted for dispersion at times other than that during the principal or dispersion phase. This is an economy for the species since restriction of dispersion to a single means, through a single agency, or all at one time might prove disastrous to its perpetuation. Because of this adaptation or ability man may exercise certain measures of control, but may not, as a rule, expect to obtain perfection or total control. This factor is, doubtless, one of the greatest weaknesses of quarantine measures.

Man has obtained some degree of control over some organisms by taking advantage of the known mode of dispersion. According to Parman (1940) the three methods of combatting dispersion are (1) controlling or eliminating the organism at its source, (2) preventing or retarding movement, and (3) resisting the establishment of the organism.

Further understanding of distance dispersion may be given by listing agents and means by which organisms are dispersed. A well organized summary of the agencies and methods of dispersion of plant pathogenic fungi was given by Heald (1913). This was followed by Gardner's (1918) more extensive treatise of plant pathogens, and by the resumé of some relationships and problems of insect transmission of disease organisms. Slight changes and modifications of these lists are made as necessitated by considerations of other organisms. Further modifications and additions are necessary to include man's agents of transportation. Moreover man's present agents of transportation providing more rapid means and frequent journeys are generally considered to be more significant modes of organismal dispersion than were those of former years.

List of Means or Agents of Dispersion.—A list of the principal means or agencies of dispersion includes:

Movement by internal source or energy—active dispersers:

- Flying
- Crawling
- Walking or running
- Swimming
- Propulsion:
 - Ejecting
 - Dehiscing

Movement by external source of energy—passive dispersers:

- Wind or air currents
- Rain or dew, atmospheric moisture
- Water currents, rivers, oceans, lakes, ponds, irrigation, water supply, sewage
- Other organisms (than man)
- Earthquake, land slide, geologic disturbance

Man as the dispersion agent—articles of commerce, products:

- Fruits
- Seeds, nuts
- Vegetative organisms, roots, tubers, corms, bulbs, rhizomes, cuttings
- Nursery stock, scions, seedlings
- Soil, litter, compost, scrap iron
- Crude products, hay, straw, grain, packing material
- Manufactured or processed goods
- Timber, lumber, logs, mine props, forest products, pulp wood
- Stone, masonry, or masonry products
- Agricultural and structural operations, planting, cultural operations, harvesting, threshing, ginning, processing

Transportation, or carriers:

- Airplanes
- Automobiles
- Barges
- Boats or rafts
- Foot traffic
- Projectiles, rockets
- Railways
- Ships
- Truck or trailer
- Vehicles, horse-drawn or otherwise.

A mechanistic mode of dispersion is recognized by the entry of organisms in or on agencies of transportation. Organisms dispersing by this means may be termed "hitchhikers." Characteristics of such dispersion include the following:

A. On the part of the organism:

1. Its entry on or in the transportation medium:
 - a. As a visitor in a temporary resting place
 - b. About the source or origin of the species
 - c. A short time preceding the start of a trip
 - d. A lasting attraction for the vehicle or carrier absent

B. On the part of man, or the carrier:

1. Usually no knowledge of access of the organism
2. No immediate deleterious effect of transporting the organism.

The importance of this mode of dispersion is evident and counteracted by the quarantines, disinfestation, disinsectization and other efforts of governmental agencies and others interested in and responsible for the prevention of movements of organisms to areas not known to be infested with them. The extreme urgency of care to prevent such dispersion is also pointed out in the book by Soper and Wilson (1943), describing eradication measures of *Anopheles gambiae* in Brazil, and in the article by Whitehead (1939) dealing with air transport and problems involved.

Increasing numbers of organisms in areas hundreds of miles from any known area of distribution are often construed as evidence of far-flung dispersions. This, in relation to the increasing rapidity and frequency of travel, has been considered of great significance. In view of the accelerating air travel increased numbers of dispersing and invading organisms may be expected. Air travel for passenger and freight service offers many chances for widespread dispersion. The improved means of air transportation move articles of commerce more quickly, frequently, and distantly. Organisms may move in like

manner whether as "hitchhikers" or in association with produce or commodities. An equalization or distribution of species in all parts of the world wherever they may find suitable food and other means of livelihood must be in a stage of accelerating progress.

In the equalization process an obligatory characteristic of dispersion is that the organism must terminate movement in a living or viable condition. The alternate of the living or viable condition, obviously, is mortality or death, and cannot reproduce the species. A corollary of dispersion, therefore, is that unless life or viability is retained through initiation, during, and for a time after termination there has been no dispersion. Although many initiate or begin dispersion and many perish during the process a few are usually or often successful and begin reproduction in a new area.

A problem confronting organisms following termination of their dispersion is that of establishing themselves. Favorable conditions for growth and reproduction must exist for success. The successful establishment of dispersed organisms, according to Waller (1918), "... including invasion and competition, the latter implying dominance, are the direct results of the interaction of climate and soils upon vegetation."

Agency Evaluation.—An evaluation of the various agencies affecting dispersion would be valuable information. More effective control of many organisms would doubtless become feasible. Since a species disperses or is dispersed by a principal means others are often of little or no value to them. Literature dealing with a species or group of closely related species may be expected to give information concerning their particular modes of dispersion. An example is the publication by Brown (1938) concerning cotton, *Gossypium*, which includes dispersion of seed and of pollen. A brief general discussion, however, is given with reference to spores, seeds, pollen, and insects on the evaluation of agencies.

Winds, or air currents, are the most effective but also the most indiscriminate of dispersing agents. More passive disperser organisms, probably, are moved by wind than by any other agency. Many active disperser organisms, however, are affected by wind and remain inactive, at rest during strong winds. It is one of the most wasteful of agencies, from the viewpoint of the number of disseminules moved, of all modes of dispersion. Wind moves small or buoyantly light organisms more effectively than heavy or bulky types.

In consideration of the number of species, those that fly, crawl, swim, walk, run, or wiggle are most abundant. They also utilize the most discriminate and less wasteful modes of dispersion.

Water currents appear to be less active as a dispersing agent than wind. Water-borne disseminules dispersed by streams move in definite directions. In oceans, gulfs, harbors, lakes, or ponds, however, wind may affect the direction of dispersion. Great distances may be covered by water-borne organisms. The coconut fruit is a classical example of an organism seen at great distances from the apparent origin. Some organisms sink in water, fresh or salt, soon after being cast thereon; others, although they float, soon lose their vitality. This is more especially true if the water is salt and rough. The coconut fruit

in salt water loses its viability within a few days through absorption of salt water, hence a new land at a great distance is unlikely to be invaded should it be cast where conditions are favorable for its propagation.

The order of effectiveness of dispersion agencies was estimated by Coulter et al. (1911) on the plants of Krakatoa Island. The first plants, after destruction of all vegetative life, stemmed from air-borne disseminules. After 15 years 60 per cent of all the plants had arrived by ocean currents, 32 per cent by wind, leaving 8 per cent which had arrived by animal agencies.

Density Levels at the Source

The effects of density levels at the source are regarded as important factors regarding the distance of dispersion. In connection with the rates of dispersion or incidence, a knowledge of the effects of different density levels of organisms is also desirable. A beginning has been made toward understanding the significance of different densities of disseminules at the origin. An adequate understanding of the relationships of distance and different population densities in dispersion, however, requires much more work under wider ranges of conditions. The literature reveals a lack of agreement in general statements on this subject and, to some extent, the data contained in it also do not agree.

The eradicator sprays applied to orchards for the control of apple scab by Keitt et al. (1937) (1941) are assumed to have provided some though not a perfect measure of control in the treated orchards. The disease incidence rate in the treated orchard at distances from an untreated orchard was clearly demonstrated, as is shown in fig. 6E. The high initial ascospore population density in the untreated orchard was sufficiently great to show considerable differences attributable to distance effects regardless of the degree of control obtained in the treated orchard. Within reasonable limits the disease incidence rates were probably the same in the treated orchard, as if the control were perfect. The technique employed is deemed an important and significant feature. In many or in most instances, as is also pointed out elsewhere in this review, only rates of decline or relative numbers of disseminules at different distances from the source may be obtained from field observations on dispersion.

The regression curves on dispersion of the anguomoiis grain moth, for example, tended to intersect at zero near 800 feet, fig. 27A, from the source regardless of high or low initial population density. Seed fall of the Douglas-fir tended to reach zero at near 650 feet from the source trees regardless of "heavy" or "light" crops, fig 11D. In a small degree the data by Romney (1939) on the incidence of curly top disease, fig. 2A, also indicated a tendency to approach an intersection at a low incidence rate. Clark (1937), in a splendid work on mosquito dispersion, concluded from his experience that "a small brood of *vexans* will fly as a large brood." In response to questions as to how far mosquitoes will fly Headlee (1937) stated, on the contrary, that "mosquitoes will move much farther if they [density of brood] are dense than if they were scarce."

Most of the evidence seems to show, however, that more distant dispersions

occur where the populations at the origin are denser. The tendency of many or most regression curve segments, figs. 5D, 8B, 9C, 13E, 15B, 17A, 23E, 32D, 38D, 40C, and 40D, to be isoclinal supports this claim. Additional evidence is gleaned from the results published by Neiswander and Savage (1931) on dispersion of the European corn borer (see fig. 47C). These results

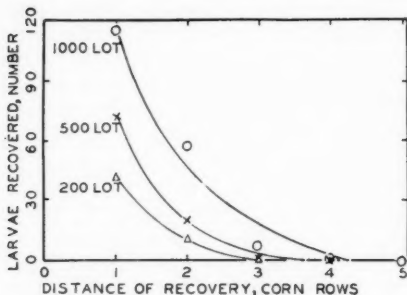


FIG. 47C.—Distances dispersed by different densities of European corn borer larvae (data from Neiswander and Savage).

show the degree of magnitude obtained from their experiments. No dispersion of European corn borer larvae beyond 3 corn rows was found with 200 egg populations at the source, none was found beyond 4 rows with 500 eggs, and none was found beyond 5 rows with 1,000 eggs at the source (see fig. 47C).

Smoothed curve values for the 200, 500, and 1,000 egg population densities show that zero infestations were reached at near 3.1, 3.9, and 4.4 rows, respectively. There is a falling off in the distance dispersed by increased population densities. This reduction follows some pattern other than an arithmetical one and is likely to assume some form of logarithmical regression.

Two explanations are given for increased distance with increased initial density levels. The more probable one is that in a larger population certain individuals are endowed with powers for more distant dispersion, or by chance occurrence some individuals disperse to greater distances than any in a smaller population. The explanation is that the increased distance dispersed by some individuals in a more dense population is a reaction to over-population. This reaction may be a very significant factor under certain conditions, in certain distance ranges, with certain species, or with combinations of factors or conditions.

Water droplet dispersion data given by Faulwetter (1917) were selected as an example of comparative density levels at the source to show more distant dispersion. Obviously this example affords only a comparison of organisms and non-organisms by analogy rather than homology.

Drop size of 0.02, taken as the base unit, is compared with drop sizes of 0.04, 0.06, and 0.10 cc., which are 2-, 3-, and 5-fold greater than the base unit. These are considered as 2-, 3-, and 5-fold more units at the origin than the base. For graphic illustration the number-of-fold-greater units than base is taken as the independent variable, or x-axis, and the mean distance (the maximum distance might have been used) of droplet splash as the dependent variable, or y-axis. Regression curves were drawn (frechand) for these observations, for

drop falls of 1, 2, and 3 feet. These drop-fall distance classes, although they possess different inherent energy values, may be considered repetitions and are presented as three curves (see fig. 47D).

Multiplicity of units at the origin is shown to increase the mean distance of water-droplet dispersion. In the observed range of unit increase over the base units, 2-, 3-, and 5-fold, the dispersion distance is increased somewhere near $\frac{1}{4}$ or $\frac{1}{3}$. If the curves be drawn from their 2-fold points to zero the distances of dispersion would apparently be increased markedly from zero to 2-fold, less markedly between 2- and 5-fold, and an extension beyond would taper to slight increases. The water droplet splashes, illustrated in fig. 47D, shown in uniform graph spacing were found to follow straight line trends if the times-greater-than-base units, or x-axes, were changed to logarithms.

The data from Neiswander and Savage (1931), fig. 47C, in which 200 larvae were the base unit make the units of 500 and 1,000 larvae $2\frac{1}{2}$ - and 5-fold greater densities. For graphic illustration the expected zero distances of 3.9 and 4.4 rows were taken for the 500 and 1,000 larval units, which with the $2\frac{1}{2}$ - and 5-fold greater initial densities were plotted in fig. 47D. Although these are but two points easily connected by a straight line an extension of the curve to zero gives a curve.

The regression curves of water droplet splashes and European corn borer larvae, comparing distances dispersed charted against initial population densities, have surprisingly similar curvatures. Analogous rates of distances dispersed on multiplicity of initial population densities are shown in curvilinear relationships. Doubling, trebling, and quintupling the units at the source increases the distance dispersed, but the rate of increase diminishes with each increase of the original population. Distances appear to be affected little by increases greater than 6-fold.

A practical consideration association with manifold initial populations and distances dispersed is that once a dispersion rate of an organism is determined a doubling, trebling, or quintupling of the population would be expected to increase slightly the distance dispersed. More reliability is suggested by this consideration for already well-founded dispersion rates. It may assist in the establishment of other dispersion rates of organisms.

Further studies are needed to determine whether organisms follow the same or similar patterns illustrated in fig. 47D. Critical measurements are needed for the evaluation of different factors.

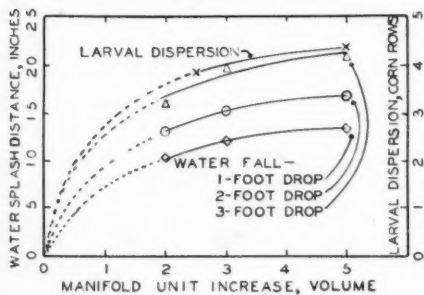


FIG. 47D.—Distance of dispersion of increased numbers or amounts over base units (data from Faulwetter, and from Neiswander and Savage).

Organisms often appear to surmount extreme barriers in accomplishing dispersion. Probably the great numbers often produced at the origin and initiating a dispersion account for the fact that a few are successful in establishing themselves as examples of frequency. The extreme barriers are, therefore, apparent rather than real. Successful dispersion of apparently stationary species of plants was observed on the oceanic island of Krakatoa, whose vegetation was destroyed by volcanic action in 1883. Unusual opportunities were afforded for studies of organisms invading it afterward. A report given by Coulter et al. (1911) indicates that, "... on Krakatoa, a quarter of a century has been long enough for the invasion of a number of species with apparently immobile disseminules, whose mode of migration is unknown."

Sampling Characteristics

Various methods have been used and are needed to measure the dispersion and incidence manifestations as related to distances. Numerous problems are involved in these processes and their solution is important to obtain a clear understanding. A few of these general problems and their characteristics are indicated.

Dispersion Equalization in Time Sequences.—Obviously some time must elapse between the initiation of dispersion and the measurement of the distances moved, because untimely observations may affect the results considerably. Two examples are used for illustration of the principle involved, although data in other examples were suggestive of effects attributable to the time elapsed.

Differences were shown by the data from McQuilken (1940), fig. 12C, on the number of pine seedlings after 1 to 3 and 4 to 12 years time. At a distance of 2.3 chains from the seed source there were 209 more seedlings after 4 to 12 years abandonment than after 1 to 3 years, based on expected numbers. At a distance of 5.8 chains there were 163 more seedlings after 4 to 12 years than after 1 to 3 years time. A longer time period favored the nearer distance with more seedlings than the more remote distance. This suggests that the efficiency and value of pine seed trees for natural stocking after 3 years is very slight. Part of this difference may be explained by the above discussion on density levels at the origin.

According to the data from Markovich (1941), fig. 33B, on mosquitoes a longer time period favored the more distant points. This is shown by the percentage values (0.10 mile was taken for the given "nearby" distance) as follows:

Distance from breeding source (miles)	Time of collection		
	Early	August	September
0.10.....	84	69	55
1.00.....	13	26	30
2.75.....	3	5	15

Movements of the host animals and the physiological state of the insects were given in explanation for the higher percentages of mosquitoes at greater distances from the source of breeding. It is suggested, however, that longevity of the insects tended to provide time in which the population became more equalized over the observed distance range. In his classical report on dispersion of the housefly Parker (1916) pointed out that the limits of dispersion must consider the length of life of the fly. Longevity of life or viability must, therefore, be considered with organisms in general.

Equalization processes are seen operative in dispersion studies. With most organisms the processes may be expected to exhibit behavioristic patterns similar to the values tabulated above. More dispersed units are expected to accumulate at the more distant points with increase of time. Longevity or viability and speed of dispersion considered in connection with the objective sought appear to govern the time lapse necessary for use in the design or procedure of dispersion experiments.

Radial and Tangential Dispersion.—Studies of the literature revealed that the dispersion or incidence data were sometimes restricted to localized sources and sometimes multiple or widespread sources. Dispersions from a localized source may be considered radial, and dispersions from widespread sources may be considered tangential dispersions. The dispersions of organisms are actually of one type—radial—although the disseminules may have followed unknown tortuous and meandering routes between the source and end points. Studies on dispersion of organisms which may originate from several and widespread points are necessary and give valuable information. The only requisite is that of recognition and differentiation between types for interpretation of the results.

Examples of rather definite sources of organisms are illustrated by the publications by Posey and Ford (1924), fig. 9C, where incidence of white pine blister rust infections was associated with a source of spores dispersing from ribes plants at a central location, and by the experiments reported by Bishopp and Laake (1921), figs. 36B, 36C, and 36D, in which flies were released at a point. An example of tangential dispersion and of the magnitude resulting therefrom is taken from the report by Porter.

A diagram from the data given by Porter (1935) may illustrate tangential dispersion. The experiment was essentially a row of 10 plants of seed from potato calico infected plants having on each side of it seed planted from healthy or non-infected plants. The non-contaminated seed were planted in five rows on each side of the contaminated seed, each row of which had 10 plants or hills. Cross-rows of plants up to five rows distance from the inoculum source row were at right angles to it. The inoculum source row is represented by S—S', fig. 48A, and the healthy plants by $H_1, H_2, \dots, H'_2, H'_1$.

H_1	H_2	H_3	H_4	H_5	H'_5	H'_4	H'_3	H'_2	H'_1
X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	X
S	—	—	—	—	—	—	—	—	S'

FIGURE 48A.—Diagram to illustrate radial and tangential potato calico incidence in potato plots.

A unit of inoculum originating in the source row, under H'_3 for example and terminating in any plant under H'_3 would be termed radial dispersion. If, however, the inoculum originated in any other row but terminated under H'_3 it would be termed tangential dispersion.

More units of dispersion might be expected to terminate under H_5 and H'_5 , or the middle, than in the marginal or outside rows. The data given by Porter (1935) confirm such an expectation. The number of potato calico infected plants in the different rows at right angles to the source rows were combined and illustrated (see fig. 48A).

Almo twice as many infected plants were observed in the fifth (middle) rows as in the second rows from the margin. The number one, or outside rows, with their larger number of infected plants than rows two and three may be the outcome of vector concentrations on the outside or border rows of the experimental plots. Rather marked effects of tangential dispersion are observed if the increased numbers of infected plants in the outside rows may be overlooked as vector concentrations.

In connection with the discussion of radial and tangential dispersion and also with epidemics a theory often accepted is that excessive reproduction of organisms occurs in a more or less restricted area and that through radiation of organisms or zonation effects distinct evidence of focal points of origination is given. In this connection also the term "source" with reference to invasions was considered ambiguous for the fruit-fly by Ripley et al. (1940) since it may refer to the place where the flies develop or to the situation occupied by them immediately before the invasion. This situation may be merely a favored place for feeding or shelter for large numbers of the flies. Furthermore, unequal development of organisms in an area, perhaps by overcrowding, quantity or quality of food change, temperature, humidity, prevalence of other organisms, or other factors, may affect the amount, time, and, to a lesser extent, the rate of dispersion. A false conception of the source or of distinct foci may be obtained. Epidemics may arise simultaneously from widespread or multiple sources as indicated by Schwerdtfeger (1943), who also suggested that several factors and their interrelationships should be studied for the explanation of organismal outbreaks.

Since recognition of the origination, or focal points, of very dense populations of organisms may often provide vulnerable openings for their control they should be observed wherever possible. Evidence of definite foci may be destroyed by equalization of organisms over widespread areas after considerable time passage.

Organismal Dispersion and Injury or Disease Incidence.—It is sometimes necessary or desirable to determine the dispersion rate, other times it is necessary or desirable to determine the incidence rate. It is sometimes essential or desirable to use one stage, generation, phase, or activity instead of any other. References to two species of fungi from the field of forest pathology offer illustrations of different methods for determining the distance relationships of two diseases.

Dispersion studies by Rankin (1914), Anderson and Babcock (1912), and Heald et al. (1915) on the chestnut blight fungus showed comparative num-

bers of spore colonies at distances from the source. These studies were conducted under different conditions, and established the fact that the inoculum was not only wind-borne but that the rate of spore dispersion decreased quite rapidly. The next step, the practical one, should have been an estimation of the distance relationship between the inoculum source and the number of trees that became infected. However, considerable search failed to disclose any publication showing an incidence rate of infected trees as related to an inoculum source.

The organism causing the Dutch elm disease, *Ceratostomella ulmi*, was reported by Smucker (1935) to have been restrictively dispersed by air currents, from 5 to 40 feet, in a closed room. Although this fungus is considered to be an insect-borne organism, estimates of spore dispersion were obtained by air currents under laboratory conditions. Incidence rates of infected trees under field conditions were reported by Zentmyer et al. (1944), and data on the subject were given by Collins et al. (1940) (see figs. 6C and 6D).

The question of measuring potato late blight disease incidence by percentage of plants infected or by numbers of lesions per plant at distances from the inoculum source may arise as with the data by Bonde and Schultz (1943), fig. 5D. The use of percentages is limited to a maximum of 100 whether the plant has but one lesion or 300. This is, in effect, a qualitative measure since one lesion on a plant may bear as much weight as 300 lesions. Comparing 293 lesions at 100 feet with one lesion at 600 feet is, however, a quantitative measure rendering equal weight indicating the change caused by the distance factor. The latter measure of dispersion is, therefore, considered to give the more nearly correct estimate of disease incidence. The curve form of the quantitative measure with its steeper slope, considered with other incidence or dispersion curve, moreover, confirms the latter method of measurement.

Sampling requires consideration of several factors. The more important are, (1) units at given distances, (2) density at the source, (3) level of organism sought as the objective, (4) impediments, (5) environmental, and (6) characteristics of the organism.

Unit Area Basis for Results.—On a theoretical basis the use of the third degree of magnitude, unit volume, may appear desirable to use for dispersion results. On a practical basis, however, most authors have presented their results in terms of the second degree of magnitude, square units. After reviewing hundreds of publications on dispersions of many organisms the suggestion is here made that unit areas of surfaces be used. In concluding their work on pollen dispersion Dahl et al. (1942) stated that, "... atmospheric pollen concentration can be expressed on the basis of number of pollen grains per unit of surface." It is admitted, however, that certain objectives may be attained only by determining or reporting the number of organisms per cubic unit.

Constants of Dispersion.—Formulae or constants have been suggested in order that basic principles of dispersion may be more completely understood. Examples of formulae for fungus spores as given by McCubbin (1943) and for pollen grains by Dahl et al. (1942) refer to passive disperser organisms. These formulae are based on measurements of the organisms involved. They

attempt to measure the rates of fall in still air through relating the size of the organisms to the time required for their descent. An equation was given by Glick (1939) for determining the aerostatic, or lighter-than-air coefficient of insects. This coefficient equals a constant multiplied by the quotient of the metric area units of the insect that are perpendicular to gravity, divided by the milligram weight of the insects. The height to which an insect may be carried by air currents is determined, according to Glick, by its size and weight, or buoyancy. The presence of insects collected at higher altitudes, 6,000-14,000 feet was attributed to their buoyancy.

Some value may result from the use of these formulae, although admittedly several factors should be considered in connection with their utilization. One factor deserving most serious consideration is that constants, those for biological phenomena, are not constant but are variable. An ideal objective would be the evaluation of the various factors and the part performed by each in affecting dispersion. For practical considerations, however, the observed numbers of dispersed organisms at distances from the origin which are affected by as many factors involved as may possibly be studied are a worthwhile goal. More direct and objective trends of dispersion or incidence studies appear in the publications by Van Zwaluwenburg and Rosa (1940), Frampton et al. (1942), Bitancourt and Fawcett (1944), Wadley and Wolfenbarger (1944), and Russell (1945).

Operative Distance of Attractiveness.—This factor has reference to those organisms which have some voluntary control over their dispersion. It may be termed "convergence" and considered an activity which is the reverse of dispersion.

Parker (1916) and Bishopp and Laake (1921) who trapped flies for their recovery results were able, by means of attractive baits, to recover part of their released flies. One might question, without detracting from their results, how much if any of the distances dispersed might have been influenced by the attractiveness of the baits. They have, however, essentially answered this question. Parker (1916) reported that "... breeding and feeding areas are not necessarily areas which attract flies and retain them, but that they may be considered substations, so to speak, which aid and abet distribution and further increase the final radius of dispersion." It was reported by Bishopp and Laake (1921) that "many apparently favorable feeding and breeding places were passed in the course of migration. ..."

Centers of attraction must also have been evident to Kligler (1924) from his studies on mosquitoes in which "... the distance of spread of Anophelines from their breeding-place appears to vary ... inversely with the density of the settlements in the neighborhood of the breeding places."

Imprisoned or Free Organisms in Dispersion.—Three methods or techniques for studying organismal dispersion are in evidence. One method is the collection, marking, release, and recovery of as many marked specimens as possible from among others of the kind. Another method is the release of organisms in an area not inhabited by the kind liberated. The third method is the enumeration of units at distances from a prolific source of the organisms.

The first two methods may be classified, according to Eyles (1944) as "experimental" and the last one as "observational."

Advantages and disadvantages are obvious with each method. With the first given method the results may be affected by the collection, confinement, and marking of specimens which reduce the amount of energy that might otherwise be spent on dispersion. Some organisms, on the other hand, might disperse to greater distances instead of less. Another disadvantage is that unmarked specimens may be, and usually are, encountered during the search for marked ones and must be separated from those liberated. The principal advantages are that dispersions occur among others of its kind, and that the positive source of organisms is known. Release of organisms in an area not known to be inhabited by its kind may provide unsuitable living conditions which would permit the results to be questioned. Also, the question of whether or not progeny of the organism would become so abundant as to constitute an economic problem would arise. Enumeration of specimens at distances from a prolific source has the disadvantage in that outside or unknown sources may contribute to the measure of the dispersing population under observation. It has the advantages of more "natural" conditions, is usually a practical one, and denser populations at the source may be readily available.

The selection of the method to be used will depend on the conditions accepted, the problems involved, and the objective to be attained. Since most field problems assume that natural conditions are involved the utilization of a centralized source of free organisms appears advisable. Reasonable care to determine and measure dispersion with relation to major sources of disseminules appears to have given satisfactory results. After using the method of collecting, staining, releasing, and recovering mosquitoes Smith et al. (1941) changed to the method of collecting them at distances from apparent sources, with more satisfactory results. Sources of minor populations seem to exert little, except possibly local, influence where the evidence shows a principal source of organisms is in existence.

Aided and Unaided Dispersion.—A classification of the modes of dispersion may divide them into aided or "artificial," and aided or "natural" means of movements. Aided or "artificial" means of movement include machine, or man-made methods by which dispersion is accomplished. It is these dispersions that quarantines attempt to eliminate or to control. Although data are unknown that illustrate the rate of dispersion by this means it is expected that the frequency of such distributions would assume patterns in which most organisms would be found nearer the source and fewer with each succeeding increase of the distance from the source. It is expected that uni- or bidirectional patterns would be more frequent along the way of most traffic, rather than omnidirectional.

Unaided or "natural" means of dispersion include movements accomplished by self propulsion, or by means of agents other than man. Unaided means of dispersion are by far the more important of the two. Man exerts but little influence over the dispersion activities of most organisms. Certain disease producing organisms, however, may depend almost wholly on man's movements for dispersion.

Continuous and Discontinuous Dispersion.—The terms, "continuous" and "discontinuous" by Butler (1917), and "regular" and "sporadic" by Fletcher (1925) have been used in reference to dispersion. These may refer to organisms that enter areas as immigrants in extending distribution or as epidemics in areas periodically infested with greater or less frequency. Whether organisms disperse voluntarily or are dispersed involuntarily by agents such as wind, water, or other organisms a diminution in the number of units with increase of distance is the regular, usual occurrence. Intermediate units connect "continuous" and "regular" dispersions. As the units become fewer in number and wider gaps occur between units we may observe "discontinuous" and "sporadic" dispersions. Numbers of units, or frequencies, are more common in the former pair of synonyms and less common with the latter pair of synonyms.

New units of dispersion occur outside of the origin and follow rather definite patterns of distribution indicating a progressive order. These units are adjoined by others and may assume a spotted effect. They may become numerous as described by Wellman (1935), or they may intensify and become epidemics, principally by secondary or later cycles or generations, in a manner discussed by Fracker (1936). These units would be more frequent around the origin and less frequent with increasing distances from the origin. More dense populations at the origin would increase the number of units and would also increase the maximum distance to the most remote unit. This problem was also encountered by Newhall (1940) in his studies on onion mildew.

Individual and Collective Dispersions.—Dispersions may be placed in one of two divisions, based according to whether the organisms disperse individually or collectively. Individual dispersions are those in which organisms are motivated to move singly, i. e., without reference to others of their species, generation, phrase, or group. Individual dispersions have been well described by Jackson (1941) with reference to tsetse fly populations. The apple maggot fly studies by Phipps and Dirks (1932) indicate individual dispersions. Since the males are believed to fly about without regard for each other the recovered gypsy moths reported by Collins and Potts (1932) are termed individual dispersions, although the female of the species is the objective purposely sought. Individual dispersions include any mass movements that are mechanistic or non-socialized.

Collective dispersions are considered those in which organisms are actuated to move in groups, more or less together and at the same time. This division might include movements that are teleological. Honeybees in swarms move collectively, unified by colony organization. Pollen and nectar gathering honeybees, on the other hand, probably disperse individually. Different swarms, however, disperse apparently without purposeful regard for other swarms.

Portion of Organisms Recovered.—All references under this heading belong to members of the Class Insecta since no records were located on any other organisms in the groups covered by this work. In no case were all of the released organisms recovered.

The percentages of fly recoveries computed from the data given by Bishopp and Laake (1921) exemplify fly recoveries of varying percentages for different distances and different species. The data are presented in tabular form, table 4.

TABLE 4.—Percentages of fly recoveries in different distance ranges.

Fly species	Midpoints of the distance ranges (miles)		
	1.45	6.15	12.40
<i>Cochliomyia macellaria</i>	21.22	0.83	0.04
<i>Phormia regina</i>	2.17	—	0.67
<i>Musca domestica</i>	30.49	0.19	0.02

A study of the data with reference to species indicates, by rank, more widespread dispersion of species in the following order, *P. regina*, *C. macellaria* and *M. domestica*. The data show marked reductions with distance increase. They suggest that this or a similar method might be used in the study of dispersions under certain conditions. Of greater biological significance, however, is the necessity for the existence of many organisms, or units, at the origin in order to increase the likelihood or expectancy of obtaining other than zeros at the more remote distances. Conversely, an application to insect or disease control would be the emphasis one could place in reducing the concentrations of insects and disease organisms at the source.

Zero Recoveries or Fewer Units of Dispersion at Greater Distances.—It is evident from the above considerations that care is required to obtain significant data at greater distances. A brief discussion was given above regarding the angoumois grain moth and the reasons for lack of observations at greater distances. Similar discussions might have been given concerning other species; the angoumois grain moth, however, serves as an example. Since the observations were for the most part within 1,000 feet of the source of moths one might ask the reason for lack of observations at greater distances. Three possible reasons are given, (1) insufficient size of fields for more distant observations, (2) at greater distances the moth source was unknown or questionable, and (3) the necessity for examining much grain in which so few moths were found that search at greater distances was abandoned as impractical. The latter reason may be the more accurate one.

Examinations of the regression curves, Part I, show that some curves have little curvatures and that others have much curvature. The curves with little bending may, in most cases, indicate that a straight line portion of the real regression distance range was under observation. Observations made over extended distance ranges would probably show more curvature. Those curves which bend more sharply are believed to indicate, as a rule, more complete covering of the distance ranges.

Observations extending over greater distance ranges reach lower incidences, or fewer units of dispersions, beyond which little or no marked changes are evident (see figs. 6B, 11D, 14A, 29D, and 35D). The determination of the feasible distance to which observations should be extended depends on the

organism and on the objective sought. Observing and determining the distance range until the regression curves bend, then flatten, and tend to approach zero dispersion or incidence units is a practical goal to attain in more critical dispersion and incidence investigations. Some preliminary knowledge of the distance range involved is desirable or necessary for conducting more critical tests.

The suggestion by Huffaker and Back (1945) that more sampling units are needed at points more distant from the organismal source is not recognized in foundations of biological and statistical aspects, provided sufficient samples are taken over the entire distance range. The taking of more and/or larger samples at more distant points, however, may give greater satisfaction and security that correct estimates are obtained. More and larger samples at the more extreme distances with fewer and smaller samples nearer the focal point may be found satisfactory. Further study and consideration are suggested for guidance in applying this procedure.

Dispersions for Control Measures

Control efforts, as indicated in the Introduction, cannot always be expected to consider the maximum distance of dispersion. Partial or fragmentary man-made efforts, however, are not only justified but need more widespread application. The ultimate goal of such efforts is that substantial reductions or delays of dispersing populations may result. In the positive direction, as for increased seed or pollen dispersion, man-made efforts may provide local increases. Control measures based on the utilization of dispersion information may be considered as impossible, impractical, possible, practical, necessary, or otherwise described. Eyles (1944) employed the terms, "effective," meaning the distance dispersed by a species in numbers to have significant importance, and "maximum," the most extreme case of dispersion to distinguish control practices.

Control efforts are most effective which begin at the source of the densest populations and extend radially outward. Recent and current measures to control the migratory grasshoppers and Mormon cricket epidemics include this means of attack. Administrators of funds and producers of commodities or services recognize that the costs of controlling an organism depend on the areas treated. The size of the areas over which it is necessary to exercise control measures depend on the square of the distance dispersed by the organism. Scraping off the bark and banding apple trees in supplementary control of the codling moth may, for example, be performed with profit to a distance of 300 feet around a fruit packing house, whereas it would cost 16 times as much to treat trees to a distance of 1,200 feet, provided the area of a complete circle about the packing house is considered. With increases in distance the costs increase and the benefits derived therefrom decrease through the "law of diminishing returns" until further control is impractical.

The shortest distance about a source that is necessary to provide control measures in order to accomplish a given objective is that at which to cease control operations. Since there are numerous factors involved in the dispersion of any species it is obvious that the more completely understood and evaluated they are the more effective and efficient the results obtained will be. More

thorough studies are, therefore, deemed essential in order to formulate dispersion objectives and execute their provisions.

In view of the fact that organisms may disperse extreme distances under unusual conditions and that means of transportation offer increased opportunities for dispersion more careful considerations should be paid to the formulation and enactment of quarantine measures. The theory of quarantines accepts the likelihood of dispersion from a center of organismal production to an area not previously infested. Problems of establishment, however, are closely related to and must be considered in connection with quarantines.

Considerations of Vertical and Horizontal Dispersion

A characteristic of the publications containing data on horizontal and vertical dispersion is that samples representing the horizontal type cover longer time periods than do those on the vertical type. Sampling in the higher elevations, hundreds and thousands of feet, has necessarily been limited by practical considerations, often to minutes of time. Much longer time, days or weeks, is usually spent in horizontal sampling for dispersed organisms. It seems most likely that organisms spend less time at vertical dispersion than at the horizontal type.

These facts may serve to minimize the importance of vertical dispersion. They may indicate, however, incomplete understanding of vertical dispersion, especially of particular species. This is exemplified by the collection of a collembolan, *Entomobyra cubensis* Fols., by Glick (1939) hundreds of miles from its known area of distribution, Cuba.

Passive disperser organisms apparently utilize vertical dispersion more frequently than organisms which disperse actively. This suggestion is evident from figures 41A, 41B, 47C, 41D, 42B, and 42C, from various published papers, and also from the discussion by Wellington (1945b). The more specialized the dispersion ability of an organism is the less frequently it appears to be taken where it is not in control of its movements. This may be regarded as a general principle characteristic of organisms. Obviously several important implications spring from this conception.

Organisms in recapitulating their numerous generations have through the ages utilized the dispersion type that permitted their existence and reproduction. This may be largely of one type or another. There is a recognized great wastage of organisms in propagating the species, part of which occurs during dispersion, and is an expected event in the struggle for continued existence. Only part of the dispersing units is expected to succeed in attaining a favorable place in which to reproduce themselves. A biological conception of this event is that without heavy mortality one or more species might soon become dominant.

Vertical Dispersion Generalizations

Organisms such as spores, pollen, and insects decrease in abundance in vertical dispersion upward in ranges involving thousands of feet. In some instances the decrease is rapid, in others, depending somewhat on the species

involved, and also on the time or weather conditions the rate is less rapid. This may be attributed to the buoyancy of an organism which determines the height to which it may be carried. Bacteria and fungi have been found rather abundant at 12,000 to 16,000 feet, records which suggest that they attain still greater heights. Considerable data on dust particle distribution were given by Kimball and Hand (1942), and atmospheric pollution studies with special reference to the solid constituents of the air pollution were reported by Ives et al. (1936). The particle abundance of inorganic matter dispersion decreased with altitude and distance increase in ways similar to those of organisms.

Much history and development of sampling techniques were given by Proctor (1935) and Lambert et al. (1941). Further knowledge is needed on sampling for vertical and horizontal dispersion and doubtless it will be increased. Some historical developments are presented by Glick (1939) with considerable attention given to the sampling procedures used. Current work in aerobiology is classifiable, according to Lambert et al. (1941), in one or more of the five following categories:

1. Sanitary air-analysis, ventilation for hospitals, schools, industries, etc.
2. Air-borne pollen dissemination.
3. Microorganisms in the upper air.
4. Epidemiology of plant diseases.
5. Insect populations and migration in the air.

Viability of Dispersing Organisms.—An important factor to be realized in dispersion, both vertical and horizontal, but more apparent from the viewpoint of the vertical type, is the viability of organisms. Spores, seeds, or pollen grains which lose their viability, and insects which become impotent or die during the dispersion process cease to be of significance to the species of organism involved. Mortality of organisms may be expected to begin the moment of departure from the source and to continue, for various reasons, until all have perished. Certain organisms, remain viable for a short length of time. Other organisms remain viable much longer, especially if conditions are favorable. If unfavorable conditions exist, for example lethal temperatures, sunlight, or desiccating air currents, the viability of organisms may decrease with great rapidity. This is discussed with reference to insects by Wellington (1945a).

Factors Affecting Vertical Abundance.—The role of wind in vertical dispersion of organisms has in some cases been regarded as very important, in other cases questioned, and in fewer cases found to be of much or of no significance. Reduced numbers of insects were collected by Glick (1939) during calm air periods. He found that at 200 feet elevations most insects were taken during wind ground surface speeds of 5-6 miles per hour, and that at 1,000 and 2,000 feet elevations most insects were taken at 7-8 miles per hour. Higher wind velocities, 15-16 miles per hour, were related to reduced numbers of insects collected at all elevations.

These and other observations show that more regular air movements of moderate velocities must be of greater significance in the dispersion of organisms than are turbulent storms. Certain species, wind-borne plant seeds, and

other passive disperser organisms may, however, be exceptions to this generalization.

Wind velocities of different speeds would be required to move different organisms either horizontally or vertically depending on the buoyance of the disseminules involved. This is illustrated by the discussion of Wellington (1945b) regarding insects. Active disperser organisms, insects for instance, restrict or modify their dispersion activities in the wind, moving principally by instinctive impulses. Many or most insects cling to positions or remain without much flying during strong winds. This is an economy of the species since individuals would be injured or destroyed, others would be removed from food or nutritional sources, and others would be unable to become mated and thus to reproduce.

More organisms disperse in daylight than at night. Many or most seeds, and pollen are dispersible during conditions of daylight hours. Convictional air currents are, furthermore, less active at night than in the daylight and thus permit gravity to overcome the buoyancy of body masses. More insects were collected by Glick (1939) before than after dark. The time for organismal dispersion depends on the conditions of light, temperature, moisture, and other factors more favorable for their activity.

Favorable temperature conditions are necessarily associated more or less with vertical dispersion abundance of organisms. Temperatures must be sufficient for permitting disseminules to become active and become released or initiate dispersion. This depends on the species involved. The greater numbers of insects were collected by Glick (1939) during ground surface temperatures between 75° and 79° F.

Vertical Strata

In recognition of various numbers of organisms at different elevations above the earth some division of the atmosphere has appeared desirable in order to obtain greater understanding of dispersion phenomena. It is recognized at the outset that many factors must be involved in causing the differences. Some of these factors undoubtedly fluctuate considerably in affecting dispersion. Any division or classification that is attempted, therefore, may be somewhat relative.

The atmosphere has been divided into two zones, or strata, by each of three different writers, based, in part at least, on the number of organisms collected at different elevations. Each writer appears to have about the same aim, to hold similar conceptions, and to recognize the significance of such divisions, although there is some lack of agreement on where the division should be made.

In collecting sugar beet pollen Meier and Artschwager (1938) recorded more pollen grains taken at 5,000 feet elevation than at 2,000, 3,000, or 4,000 feet. They reported that 5,000 feet was in the "dust horizon." No term was given for the lower stratum.

On the basis of insect population Berland (1935) divided the atmosphere into two zones. The "terrestrial" zone was considered to extend upward to nearly 200 feet and to serve as a medium for the larger and more active disperser insects. The "plankton" zone was defined as the atmosphere upward

from the "terrestrial" zone containing the weaker flies, smaller insects, and passive dispersers.

A division of the atmosphere was suggested by Wellington (1945b). At temperatures above 45° (7.0° C.) the stratum would be termed the "active" plankton zone. This zone would include most insects, the active dispersers, and the passive dispersers dependent on vertical air currents for production and maintenance of altitude and on horizontal currents for horizontal movements. At the higher altitudes, temperatures below 45° F., most insects would be passively borne by vertical air currents. This zone would be termed the "inert" plankton zone. These terms appear to have more basis on responsiveness of organisms, especially insects which tend to become inactive at temperatures near 45° F.

Divisions of the atmosphere may have a logical basis if one considers that most organisms disperse not far above the ground, or in consideration of differences in the numbers of disseminules in the elevation by which more organisms exist at higher than at some lower altitudes in certain areas or under certain conditions in any area. Most organisms disperse nearer the ground than at 5,000 or 200 feet elevation. Most dispersion probably occurs within 25 feet elevation (see figs. 41A to 46A). Undoubtedly different factors contribute to differences in disseminule numbers at different altitudes. Increased wind velocities are generally present with height increase in free air, and cross currents of air streams may unequally affect atmospheric samples of disseminule populations taken at different altitudes.

Organismal Increase Preceding Decrease with Increased Heights.—The extensive data listed by Glick (1939), and the results given by most authors show that greater numbers of insects are found nearer the ground level, and in general decrease as the altitude increases. Spores, bacteria, and other passive dispersers, figs. 41A to 43B, show decreases with altitude increases. More Thysanoptera, aphids, and cotton flea-hoppers, however, are shown at higher elevations (see figs. 44B, 44C, and 45D). No special significance is attached to these observations since they are believed to have sought the height above ground for dispersion that was most beneficial for their movements. Had the sampling processes been continued to greater heights a peak in the abundance of insects would have been reached. It is obviously impossible for indefinite and continued increases in organisms with increased heights above the ground. Where increases are noted a consideration may be given regarding the elevation at which the population peak is reached.

Each species must seek the vertical air strata most promising for its dispersal and continued existence. Passively dispersing bacteria, for example, apparently need to disperse widely and at high elevations in order to strike favorable places for living and reproducing. The tobacco flea beetle, on the contrary, may locate favorable host plants by dispersing most abundantly at three feet heights near the site on which it emerges as a young adult.

Appendix

The regression formulae used for determining the calculated or curve values used in the figures are herewith recorded:

- Figure 1A: $E = 16.7512 - 24.1366 (\log x) + 260.8055 (1/x)$.
 Figure 1B: Data from Felt, $E = 115.6997 - 54.1268 (\log x) + 1.3563 (1/x)$.
 Data from Gaines and Ewing,
 $E = 19.9539 (\log x) + 6892.1875 (1/x) - 74.2906$.
 Figure 1D: $E = 12.2275 (\log x) + 842.6825 (1/x) - 30.4456$.
 Figure 2A: 1928 and 1929, $E = 89.5269 - 37.1108 (\log x) + 4346.6556 (1/x)$.
 1930 and 1931, $E = 544.9337 - 205.7962 (\log x)$.
 1933, $E = 287.8527 - 102.7691 (\log x)$.
 Figure 2B: $E = 66.2650 - 29.4213 (\log x) + 13.3938 (1/x)$.
 Figure 2C: $E = 36.0837 - 38.8472 (\log x)$.
 Figure 2D: $E = 67.6866 - 66.5759 (\log x) - 41.6043 (1/x)$.
 Figure 3A: $E = 16.5750 + 11.8934 (\log x)$.
 Figure 3B: $E = 137.6834 - 58.5767 (\log x)$.
 Figure 3C: $E = 253.2956 - 185.1845 (\log x)$.
 Figure 3D: $E = 5.9278 - 1.1925 (\log x)$.
 Figure 4A: $E = 10.7775 - 14.3675 (\log x) + 10.1586 (1/x)$.
 Figure 4B: $E = 69.3312 - 32.0002 (\log x) + 1097.2192 (1/x)$.
 Figure 4C: $E = 0.3180 - 0.3945 (\log x)$.
 Figure 5A: Sea-water medium, $E = 30.6843 + 14.2707 (\log x)$.
 Fresh-water medium, $E = 10.3975 + 8.0945 (\log x)$.
 Figure 5B: Sea-water medium, $E = 547.5752 + 127.7996 (\log x)$.
 Fresh-water medium, $E = 38.4606 + 33.9144 (\log x)$.
 Figure 5C: Sea-water medium, $E = 156.0661 - 50.4221 (\log x)$.
 Fresh-water medium, $E = 263.8568 - 96.6934 (\log x)$.
 Figure 5D: Lesions per 100 plants,
 $E = 149.9342 (\log x) + 49,766.4933 (1/x) - 502.4637$.
 Plants infected, percentage,
 $E = 161.1303 - 63.7467 (\log x) + 6589.6956 (1/x)$.
 Figure 6A: $E = 41.1408 - 14.7576 (\log x)$.
 Figure 6B: $E = 1511.6569 (\log x) + 16779.2264 (1/x) - 10075.7045$.
 Figure 6C: $E = 38.8871 - 11.1381 (\log x)$.
 Figure 6D: $E = 40.6518 - 17.5778 (\log x) + 843.1951 (1/x)$.
 Figure 7A: $E = 521.7569 - 214.2687 (\log x) - 682.3625 (1/x)$.
 Figure 7B: $E = 636.6122 - 284.4874 (\log x)$.
 Figure 7C: $E = 24.4802 (\log x) + 137.3053 (1/x) - 107.6430$.
 Figure 7D: $E = 2.3492 - 0.8542 (\log x)$.
 Figure 8A: High, $E = 1182.1773 (\log x) + 9877.6263 (1/x) - 2001.6244$.
 Intermediate, $E = 493.0503 - 374.3649 (\log x) - 320.8880 (1/x)$.
 Low, $E = 196.3789 (\log x) + 1212.4207 (1/x) - 314.5034$.
 Figure 8B: High, $E = 246.3689 (\log x) + 1685.9662 (1/x) - 397.6009$.
 Intermediate, $E = 67.1821 (\log x) + 700.7788 (1/x) - 121.3435$.
 Low, $E = -20.9499 (\log x) + 13.9037 (1/x) - 25.8738$.
 Figure 8C: Jones and Bartholomew, $E = 63.5594 - 23.4810 (\log x)$.
 Reed and Crabill, $E = 86.1007 - 46.1628 (\log x)$.
 Figure 8D: $E = 22.9424 - 17.0033 (\log x)$.
 Figure 9A: May 24 & 25:
 $E = 64588.1852 - 21,356.2321 (\log x) - 239819.3699 (1/x)$.
 Figure 3, $E = 34034.9962 - 9101.6854 (\log x)$.
 Figure 9B: $E = 50.7023 - 31.9056 (\log x)$.
 Figure 9C: No. and W. directions, $E = 203.2586 (\log x) - 69.3137$.
 East direction, $E = 14.8078 (\log x) + 4349.6492 (1/x) - 47.1129$.
 South direction, $E = 245.4314 - 83.0053 (\log x)$.

- Figure 9D: $E = 143.9387 - 40.8005 (\log x)$.
- Figure 10A: *Ribes lacustre*, $E = 35.1563 - 14.8359 (\log x)$.
Ribes viscosissimum, $E = 32.0656 - 14.6735 (\log x)$.
- Figure 10B: $E = 185.1634 - 96.2535 (\log x)$.
- Figure 11A: $E = 32.6495 - 27.1101 (\log x)$.
- Figure 11B: Tables II and III, $E = 17.8519 - 14.3260 (\log x)$.
 Table V, $E = 95.9794 - 109.8583 (\log x)$.
- Figure 11C: Tables II and III, $E = 30.0833 - 1.8200 (x)$.
 Table V, $E = 439.1953 - 447.6014 (\log x)$.
- Figure 11D: Heavy crop, $E = 166.3653 (\log x) + 39091.9738 (1/x) - 523.9309$.
 Light crop, $E = 77.6905 - 27.0391 (\log x)$.
 (000 omitted from the formulae in Figure 11D.)
- Figure 12A: Table I, $E = 1257.9204 - 2435.2954 (\log x)$.
 Table II and III, $E = 34.0840 - 9.8958 (\log x)$.
- Figure 12B: $E = 295.2465 - 123.1957 (\log x) - 907.9029 (1/x)$.
- Figure 12C: Abandoned 1-3 years, $E = 3349.0593 - 3722.9489 (\log x)$.
 Abandoned 4-12 years, $E = 3587.5954 - 3817.8974 (\log x)$.
- Figure 12D: $E = 339.9269 (\log x) + 1083.0515 (1/x) - 466.6477$.
- Figure 13A: Table I, $E = 4744.2163 - 9470.4905 (\log x)$.
 Table V, $E = 2171.8593 (\log x) + 1541.1073 (1/x) - 3654.8859$.
- Figure 14A: $E = 7.9354 - 2.4557 (\log x) - 26.0994 (1/x)$.
- Figure 14B: $E = 40.5998 - 26.0668 (\log x)$.
- Figure 14C: $E = 17.7854 - 5.2863 (\log x) - 0.3109 (1/x)$.
- Figure 14D: Data from Brown, $E = 0.4941 - 0.3123 (\log x) + 14.3214 (1/x)$.
 Data from Pope, et al., $E = 26.4479 - 15.0674 (\log x)$.
- Figure 15A: $E = 72.6632 - 27.5444 (\log x) - 36.9918 (1/x)$.
- Figure 15B: Table 12, $E = 0.4386 - 0.1953 (\log x)$.
 Table 13, $E = 1.8563 - 0.5095 (\log x)$.
 Table 16, $E = 10.0536 - 0.0430 (x)$.
- Figure 15C: $E = 2.7236 (\log x) + 5.4398 (1/x) - 0.7398$.
- Figure 15D: $E = 13.0469 - 12.2925 (\log x)$.
- Figure 16A: $E = 1.4221 - 0.3692 (\log x)$.
- Figure 16B: 1930, $E = 73.6707 - 15.8569 (\log x)$.
 1931, $E = 37.5045 - 2.5597 (\log x)$.
- Figure 16C: $E = 102.7996 - 2.1516 (\log x)$.
- Figure 16D: Lima, $E = 4.5967 - 3.6329 (\log x)$.
 Common, $E = 8.5340 - 5.9964 (\log x)$.
- Figure 17A: NW-SE direction, $E = 29.2295 - 18.3154 (\log x)$.
 SW-NE direction, $E = 25.3202 - 16.3074 (\log x)$.
- Figure 17B: $E = 35.2204 - 13.8707 (\log x)$.
- Figure 17C: $E = 0.2599 (\log x) + 13.2189 (1/x) - 0.5754$.
- Figure 18A: $E = 11.2306 - 2.6245 (\log x)$.
- Figure 18B: $E = 8.8937 (\log x) + 894.6842 (1/x) - 24.0611$.
- Figure 18C: Table data, $E = 4.1386 + 0.0292 (x)$.
 Text data, $E = 11.9590 + 10.6250 (\log x)$.
- Figure 18D: All leafhoppers, $E = 3816.2238 - 3676.1264 (\log x)$.
Empoasca fabae, $E = 54.5355 - 34.9395 (\log x)$.
Macrostelus divisius,
 $E = 215.1181 (\log x) + 2618.5120 (1/x) - 459.3667$.
- Figure 19A: $E = 21.1441 - 3.1562 (\log x)$.
- Figure 19B: Nevada-Utah-Colorado,
 $E = 129.3340 (\log x) + 10381.7704 (1/x) - 345.5000$.
 Nevada-Utah, $E = 288.2786 - 114.3746 (\log x)$.
- Figure 19C: Nevada-Utah-Colorado, $E = 161.0248 - 62.1579 (\log x)$.
 Nevada-Utah, $E = 42.3863 - 0.0705 (\log x)$.
- Figure 19D: $E = 10.2020 - 6.5760 (\log x) - 0.9951 (1/x)$.
- Figure 20A: Orchard source, $E = 905.4472 - 306.2517 (\log x)$.
 Bouquet source, $E = 208.2934 - 88.4252 (\log x)$.
- Figure 20B: $E = 13.1891 (\log x) - 85.6110 (1/x) + 17.3055$.

- Figure 20C: $E = 25.8748 - 8.7624 (\log x)$.
 Figure 20D: $E = 0.8015 - 0.9179 (\log x)$.
 Figure 21A: $E = 247.1612 - 125.0356 (\log x)$.
 Figure 21B: $E = 0.3417 - 0.1115 (\log x)$.
 Figure 21C: $E = 2.7272 - 18.2237 (\log x) + 4.3309 (1/x)$.
 Figure 21D: $E = 18.4622 - 4.5345 (\log x)$.
 Figure 22A: $E = 62.2152 - 4.3707 (\log x)$.
 Figure 22B: $E = 13.0351 - 16.3183 (\log x)$.
 Figure 22C: $E = 191.0463 - 56.1930 (\log x)$ (distance x in terms of yards).
 Figure 22D: Infested squares, $E = 189.9917 - 75.0475 (\log x)$.
 Weevils collected, $E = 52.3988 - 14.1418 (\log x)$.
 Figure 23A: Males, $E = 6.9900 (\log x) + 96.0701 (1/x) - 20.2653$.
 Females, $E = 20.7221 (\log x) + 109.6363 (1/x) - 51.7727$.
 Figure 23B: Overwintered adults and first brood larvae, $E = 37.8784 - 21.4056$.
 Total season, $E = 16.2558 (\log x) + 21.4046 (1/x) + 27.6124$.
 Figure 23C: Distance, $E = 6.9376 (\log x) + 3025.5199 (1/x) - 24.1944$.
 Time, $E = 28.9641 (\log x) - 42.3808$.
 Figure 23D: $E = 1.3007 - 0.5740 (\log x) + 0.1906 (1/x)$.
 Figure 23E: Table 56, $E = 358.3302 - 336.9034 (\log x)$.
 Table 57, $E = 320.4595 - 277.1802 (\log x)$.
 Figure 24A: $E = 14.9357 - 5.5210 (\log x)$.
 Figure 24B: NNE Distance, $E = 144.7505 - 49.1857 (\log x)$.
 Time, $E = 60.1870 (\log x) - 97.1355$.
 SSW Distance, $E = 330.0180 - 109.5952 (\log x)$.
 Time, $E = 28.9035 (\log x) - 42.1175$.
 Figure 24C: May 29, $E = 23.6375 - 13.6444 (\log x) + 7.3816 (1/x)$.
 June 5, $E = 18.7380 - 14.1833 (\log x)$.
 Figure 24D: $E = 8.1695 - 3.1130 (\log x)$.
 Figure 25A: New Jersey, $E = 27.94 - 8.71 (\log x) + 1276/x$.
 Connecticut, $E = 10.77 - 3.84 (\log x) + 69/x$.
 [From Wadley and Wolfenbarger (1944)]
 Figure 25B: $E = 1.8498 - 0.7537 (\log x)$.
 Figure 25C: $E = 0.0577 (\log x) + 35.0474 (1/x) - 1.7709$.
 Figure 25D: Wolfenbarger and Jones, $E = 51.1508 - 11.5808 (\log x)$.
 Whitten, $E = 1.8632 (\log x) + 46.7372 (1/x) - 2.6739$.
 Figure 26A: $E = 63.2925 - 53.2728 (\log x)$.
 Figure 26B: $E = 166.0964 - 60.4337 (\log x)$.
 Figure 26C: Lanesboro, $E = 9.1303 - 5.4109 (\log x) + 13.4155 (1/x)$.
 Allamuchy, $E = 24.4569 - 8.1431 (\log x) + 222.7513 (1/x)$.
 Figure 27A: 1924, $E = 1.3092 - 0.4440 (\log x)$.
 1925, $E = 0.1877 - 0.0625 (\log x)$.
 1926, $E = 0.0872 - 0.0268 (\log x)$.
 Figure 27B: $E = 41.5154 - 7.8286 (\log x)$.
 Figure 27C: $E = 29.3703 - 23.0838 (\log x)$.
 Figure 27D: $E = 5.2904 (\log x) + 20114.0849 (1/x) - 18.0628$.
 Figure 28A: $E = 1.8581 - 0.1852 (\log x)$.
 Figure 28B: $E = 206.2920 - 79.7554 (\log x)$.
 Figure 28C: $E = 250.8921 - 80.8036 (\log x)$.
 Figure 28D: $E = 26.8354 (\log x) + 284.6776 (1/x) - 48.8278$.
 Figure 29A: Hervey and Palm, $E = 82.4743 - 61.1711 (\log x)$.
 Ficht and Heinton, $E = 65.1600 - 83.5980 (\log x)$.
 Figure 29B: 1929, $E = 150.3706 - 61.4430 (\log x) - 134.6495 (1/x)$.
 1930, $E = 229.2502 - 117.8881 (\log x) + 633.4616 (1/x)$.
 Figure 29C: $E = 16.7966 (\log x) + 515.6276 (1/x) - 39.5778$.
 Figure 29D: $E = 1.2053 (\log x) + 918.2934 (1/x) - 4.3763$.
 Figure 30A: $E = 40.8525 (\log x) + 38124.4221 (1/x) - 151.3370$.
 Figure 30B: $E = 94.4921 (\log x) + 272732.0245 (1/x) - 404.7887$.
 Figure 30C: $E = 1614.4858 - 549.0676 (\log x)$.
 Figure 30D: $E = 13.7076 - 5.1352 (\log x)$.

- Figure 31A: $E = 95.3981 - 117.0255 (\log x)$.
 Figure 31B: 25 watt mercury vapor light, $E = 32.4015 - 1.1057 (\log x)$.
 60 watt mercury vapor light, $E = 42.2399 - 14.7333 (\log x)$.
 75 watt tungsten light, $E = 45.3340 - 11.7353 (\log x)$.
 Figure 32A: $E = 7.7333 - 1.6000 (\log x)$.
 Figure 32B: $E = 30.0036 (\log x) + 22534.5188 (1/x) - 106.5672$.
 Figure 32C: $E = 2.3300 - 3.7374 (\log x)$.
 Figure 32D: Table 3, $E = 120.6890 - 33.7089 (\log x)$.
 Table 4, $E = 126.7820 - 33.9291 (\log x)$.
 Table 7, $E = 227.6914 - 58.1702 (\log x)$.
 Figure 32E: $E = 731.8625 - 2600.9299 (\log x) + 168.4682 (1/x)$.
 Figure 33A: Table 6, $E = 115.8276 - 29.6934 (\log x)$.
 Text data, $E = 445.7016 - 117.7673 (\log x)$.
 Figure 33B: Early summer, $E = 6.6912 - 14.5316 (\log x) + 6.3077 (1/x)$.
 August, $E = 26.4627 - 48.1642 (\log x) + 0.5627 (1/x)$.
 September, $E = 31.2114 - 35.9043 (\log x) - 1.2114 (1/x)$.
 Figure 33D: $E = 7.1924 - 5.9946 (\log x)$.
 Figure 34A: $E = 14.9539 - 3.8129 (\log x)$.
 Figure 34B: Table 9, $E = 1.9037 (\log x) + 9.3423 (1/x) + 3.1020$.
 Table 11, $E = 2.9002 - 2.7237 (\log x)$.
 Figure 34C: $E = 56.1681 - 49.3604 (\log x) + 41.3496 (1/x)$.
 Figure 34D: All species.
 $E = 181099.0192 (\log x) + 610477.5996 (1/x) - 237544.0286$
Aedes sollicitans,
 $E = 179133.3492 (\log x) - 630429.9648 (1/x) - 240009.1872$.
Aedes vexans, $E = 243.1983 - 208.4554 (\log x)$.
 Figure 35A: $E = 15.6196 (\log x) + 5472.9344 (1/x) - 35.9966$.
 Figure 35B: $E = 28.5309 - 14.0733 (\log x) + 209.1368 (1/x)$.
 Figure 35C: $E = 96.1818 - 38.0044 (\log x) + 7480.0398 (1/x)$.
 Figure 35D: $E = 58.4486 - 19.5384 (\log x)$.
 Figure 36A: Table II, $E = 227.7183 - 83.6765 (\log x)$, (x in chains).
 Table V, $E = 105.0289 - 111.0214 (\log x)$, (x in miles).
 Table X, $E = 3.2675 - 2.5160 (\log x)$, (x in miles).
 Figure 36B: $E = 150.2102 (\log x) + 1549.8874 (1/x) - 268.5584$.
 Figure 36C: Table II, $E = 4.2950 - 0.9250 (\log x)$, (x in chains).
 Table X, $E = 8.4031 - 6.8862 (\log x)$, (x in miles).
 Figure 36D: Table II, $E = 524.9296 (\log x) - 49605.4083 (1/x) - 1440.2348$,
 (x in chains).
 Table V, $E = 6.2897 - 12.0103 (\log x) + 45.9126 (1/x)$, (x in miles).
 Table X, $E = 9.3852 - 8.3779 (\log x) + 4.9749 (1/x)$, (x in miles).
 Figure 37A: $E = 45.3663 - 51.5218 (\log x)$.
 Figure 37B: $E = 6.6733 - 1.7253 (\log x)$.
 Figure 37C: $E =$ Flies entering clearing, $E = 58.8611 - 23.5436 (\log x)$.
 Flies following man, $E = 51.9341 - 12.9765 (\log x)$.
 Figure 37D: $E = 104.1145 - 36.6017 (\log x)$.
 Figure 38A: $E = 0.017000 - 0.000391 (\log x)$.
 Figure 38B: Adults swept, $E = 0.9731 (\log x) - 1299.4343 (1/x) - 3.8635$.
 Ultimate infestation, $E = 159.4212 - 32.2329 (\log x)$.
 Figure 38C: Spring form, $E = 11.8272 - 6.2665 (\log x) - 13.8511 (1/x)$.
 Summer form, $E = 51.6979 - 19.3174 (\log x)$.
 Figure 38D: E. and W. directions, $E = 70.7360 - 15.5961 (\log x)$.
 South direction, $E = 55.0255 - 11.7128 (\log x)$.
 North direction, $E = 46.1645 - 11.6724 (\log x)$.
 Figure 39A: $E = 6.0488 - 0.9381 (\log x)$.
 Figure 39B: $E = 102.9827 - 32.9320 (\log x)$.
 Figure 39C: Rushland 1935, $E = 4.8913 - 1.9021 (\log x)$.
 Rushland 1936, $E = 4.6550 - 1.7547 (\log x)$.
 Philmont 1936, $E = 4.7204 - 1.1767 (\log x)$.
 Figure 39D: N. W. quadrant, $E = 26.3929 - 10.4753 (\log x)$.

- Other quadrants, $E = 15.8605 - 7.4680 (\log x)$.
- Figure 40A: 5-colony group, $E = 3.5231 - 1.9619 (\log x)$.
12-colony group, $E = 94.3842 - 43.9238 (\log x)$.
- Figure 40B: $E = 53.6131 - 33.3623 (\log x) - 55.9140 (1/x)$.
- Figure 40C: $E = 1.8473 + 27.3306 (\log x)$.
- Figure 40D: $E = 52.9285 - 17.5829 (\log x)$.
- Figure 41A: $E = 453.7434 - 107.4337 (\log x)$.
- Figure 41B: Table I, $E = 455.3601 - 87.3045 (\log x)$.
Table II, $E = 3854.0377 - 1020.2009 (\log x) + 2016.3507 (1/x)$.
- Figure 41C: $E = 5.0521 - 0.9814 (\log x)$.
- Figure 41D: $E = 0.6988 (x) - 0.3747$.
- Figure 42A: $E = 65.6091 - 38.9724 (\log x)$.
- Figure 42B: $E = 65.9928 - 15.9200 (\log x) + 531.7772 (1/x)$.
- Figure 42C: $E = 35372.9375 - 8782.7042 (\log x) + 115389.9402 (1/x)$.
- Figure 42D: $E = 53.7149 - 16.8605 (\log x)$.
- Figure 43A: Table I, $E = 1520.4892 - 400.2627 (\log x) + 4564.2050 (1/x)$.
Table II, $E = 99.3641 - 26.1220 (\log x)$.
- Figure 43B: $E = 159.3258 (\log x) - 2568.8821 (1/x) - 1278.4983$.
- Figure 43C: $E = 390.4255 - 151.1777 (\log x)$.
- Figure 43D: $E = 24.5966 - 6.1220 (\log x) + 186.5688 (1/x)$.
- Figure 44A: $E = 238.5377 - 66.9125 (\log x) + 958.4927 (1/x)$.
- Figure 44B: $E = 327.1773 (\log x) - 46.8403$.
- Figure 44C: $E = 2769.4278 - 503.1926 (\log x) - 1270.1502 (1/x)$.
- Figure 44D: $E = 0.9638 + 0.6755 (x)$.
- Figure 45A: $E = 471.3005 - 216.5135 (\log x)$.
- Figure 45B: $E = 394.6575 - 276.3679 (\log x)$.
- Figure 45C: $E = 47.0030 - 32.4075 (\log x)$.
- Figure 45D: $\log E = 1.5944 + 0.0342 (x)$.
- Figure 46A: $E = 1765.6767 - 1218.7522 (\log x)$.
- Figure 46B: $E = 26.0229 - 24.2161 (\log x) - 11.4458 (1/x)$.
- Figure 46C: $E = 636.3306 - 305.0288 (\log x)$.

Formulae:

Distance range 2.00-3.99 miles, $E = 38.7430 - 71.3603 (\log x)$.

Distance range 0.5-6.0 miles,

 $E = 293.7746 (\log x) + 440.8701 (1/x) - 276.9236$.

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Studies on Deciduous Forest Animal Populations During a Two-Year Period with Differences in Rainfall

Lucile A. Rice

Introduction

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In the fall of 1933 the writer undertook a study of the invertebrates and A. C. Twomey the vertebrates in the Wm. Trelease Woods (formerly University Woods) of the University of Illinois, a fifty-acre (20 hectare) area of woodland six miles northeast of Urbana, Illinois. Several papers have been already published on populations and seasonal migrations and other movements of the invertebrates of this forest. (See Weese, 1924; Blake, 1926, 1931; Smith-Davidson, 1928, 1930; Beall, 1935; and Carpenter, 1935).

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The purpose of this paper is to report on several aspects of forest animal populations. The period from late September, 1933, through October, 1935, offered especial opportunities for the study of temperature and rainfall effects and of coactions.

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The coaction studies were facilitated by cooperation with Mr. Twomey. A close check was kept on the birds and mice in order to determine their effect on invertebrate populations; birds were shot by Mr. Twomey and the stomach contents examined by the writer. In addition, it was possible to analyze the factors which influence migration of the invertebrates into and out of hibernation. A comparison of the work done in earlier years on the same area was also possible. Several checks were made to ascertain the validity of the sampling methods in general use.

Description of Habitat

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The area of study taken as a whole contains more elms and sugar maple than any other species of trees. Accordingly, it has been referred to as an elm-maple forest by Weese, Smith-Davidson, and others. A mapping of the climax (maple) and subclimax (elm) areas has been made by Twomey (1945). The area consists of about 20 hectares, (50 acres) of actual woodland, surrounded by cultivated fields. It has the usual woodlot edge vegetation of hawthorn, buckbush, hazelnut, and blackberry briar extending inward under the trees for 12 to 15 feet on all sides. The ground is covered by 6 or 7 inches of mulch and leaves. The herb layer (McDougall, 1922; and Weese, 1924) is divisible into the following plant societies:

Prevernal societies

Claytonia virginica
Isopyrum biternatum
Collinsia verna
Dicentra cucullaria
D. canadensis
Phlox divaricata
Geranium maculatum
Floerkea proserpinacoides

Vernal Societies

Hydrophyllum appendiculatum
H. canadense

Aestival societies

Laportea canadensis
Impatiens biflora
I. pallida

Serotinal and Autumnal Societies

Campanula americana
Eupatorium rugosum
Other Composites

The shrub layer is dominated by the pawpaw (*Asimina triloba*) which extends from 4 to 20 feet in height, followed in abundance by the spice-bush (*Lindera benzoin*), which ranges from 4 to 12 feet in height; other true shrubs are scattered. The seedlings of maple, elm, and other trees make up a considerable portion of the shrub height woody undergrowth.

The sugar maple (*Acer saccharum*) dominates on the higher ground and makes up about one-third of the area or 7.00 hectares, while the American elm (*Ulmus americana*), American ash (*Fraxinus americana*), blue ash (*F. quadrangulata*), basswood (*Tilia americana*), and blue beech (*Carpinus caroliniana*) dominate the lower and more hydric two-thirds or 13 hectares.

Methods

Collections and observations were made every 7 to 10 days from October, 1933, to November, 1935. The unit taken in shrubs and herbs was 50 sweeps of an insect net 30 centimeters in diameter (Weese, 1924; Smith, 1928). Beall (1935) made a study which showed that a lesser number of longer strokes gave a consistent equivalent to the population of 1 square meter. The ground sample unit was 0.1 square meter dug to the depth of 4 inches (10 cm.).

A sweeping check was made August 8, 1935, on sampling over a definite area. An area with the typical vegetation of nettle, water leaf, and jewel weed, which made a dense stand, was selected. An area 20 by 20 meters was measured off over an area located in quadrat N3-W1.¹ The insect sweep net was used; 125 strokes were required to cover the 400 square meters while walking at a rate of about 2½ miles per hour and making about one stroke per second, first to the right and then to the left. This was repeated to make a total of four sets of 125 strokes. This operation was to determine the following:

- a. Number of sweepings to get most of the individuals present;
- b. Whether 50 strokes secure a typical sample.

¹ Since this work was done, center of the woods was established by a careful survey and yellow iron stakes placed 50 meters apart, laying the area off into squares with their corners numbered from the north-south and east-west lines passing through the center.

The results in terms of number of specimens and species for each time the area was covered was as follows:

- 1st sweeping, 237 individuals—37 species.
- 2nd sweeping, 177 individuals—27 species.
- 3rd sweeping, 94 individuals—18 species.
- 4th sweeping, 88 individuals—14 species.

This by no means represents all of the individuals on this area. Careful examination after the four sweepings showed only an occasional specimen clinging to the vegetation, numerous Phylloxera on the wing, and many individuals that had fallen to the ground.

Only nine species not found in the first sweeping were taken in the second and no new species occurred in the third and fourth sweepings.

Table 1 gives the results of these collections by total number of individuals and species found in each of four sweepings and the numbers and percentage of each order represented in each sweeping. Many individuals had been clinging to the plants and those not caught were knocked off onto the ground by the first sweeping and not taken at all thereafter. The high percentage of specimens in some orders was due to the following: viz.

- Hemiptera, to an assassin bug (Reduviidae) and certain plant bugs (Miridae)
- Homoptera, to leaf hoppers (Cicadellidae) and aphids (Phylloxera)
- Lepidoptera, to an inchworm (Geometridae larva)

Ten days later (August 18) four sweepings of 125 strokes each over the same area gave the distribution as shown in the second part of Table 1. Again ants led the list. A black flea beetle which had been abundant on the nettle all through July and August during both 1934 and 1935 was abundant. Four immature millipeds (*Fontaria* sp.) were taken in the second sweeping. They were also found clinging to the vegetation in other parts of the woods. A nabid nymph was quite abundant during this period and was not found 10 days earlier. There was a slight difference in total numbers and an addition of two new orders. The invertebrates were just as abundant over this area which had had a large part of the population removed 10 days previous as over any other part of the woods, probably due to inward migration.

Since the area marked off required more than 50 strokes to cover it, 50 strokes were taken just outside the marked area in the same type of vegetation and compared with the 125 strokes in the marked area. The following were obtained in the 50 strokes: 120 individuals representing 34 species, in all 11 orders shown in Table 1 for August 8. Again on August 18, another 50 strokes at random were made and compared with the 125 strokes; the results were as follows: 130 individuals, representing 35 species and 12 orders. Table 1 shows that (1) a first sweeping obtains a typical sample and slightly less than one-half of the total population over the area; (2) 50 strokes secure representatives of all but the least abundant species, falling only a little short of the maximum number; (3) additional strokes increase the number of specimens; (4) 50 strokes give an approximate numerical value equal to that found on one square meter.

TABLE 1.—Number of individuals found in each of four 125 stroke sweepings over the same area of vegetation (400 square meters), August 8 and 18, 1935. The number of individuals is indicated below the column headings—first, second, etc., which indicate the order in which the collections were made.

	AUGUST A						AUGUST B					
	1ST	%	2ND	%	3RD	%	1ST	%	2ND	%	3RD	%
ORBLR	36	16.0	23	14.1	20	2.12	15	17.0	28	12.5	26	23.2
MEMIPTERA	18	9.8	21	11.0	3	3.1	31	13.9	5	6.9
COLOROPTER	10	5.7	11	6.3	1	1.0	32	28.6	26	36.1
DIPTERA	23	10.8	11	6.3	12	2.1	3	4.5	11	15.3
ANTS	86	37.6	25	14.1	30	32.0	23	26.1	34	33.2	25	22.3
HOMOPTERA	30	12.6	80	33.9	18	19.1	45	51.1	20	6.9	12	10.7
ORTHOPTERA	1	0.4	5	2.2	3	1.6
HYMENOPTERA	1	0.4	24	10.7
LEPIDOPTERA	7	3.0	19	10.7	6	6.6	5	5.6	24	10.7	6	6.3
NEUROPTERA	3	1.2	3	1.9	3	3.2	13	6.0	5	4.5
FONTARIA	4	3.6	1	1.4
ISOPOD	1	1.4
TOTAL NUMBER OF SPECIES	37	..	27	..	18	..	14	..	39	..	13	..
TOTAL NUMBER OF INDIVIDUALS	237	..	117	..	94	..	86	..	223	..	72	..

The 50-strokes method of collecting was used throughout the study. Specimens from the sweepings were anaesthetized and the invertebrates picked out of the leaves. One specimen of each species not taken in previous collections of the season was pinned or preserved in alcohol. The remainder of the collection was also preserved and retained.

Ground Sampling.—The ground sample consisted of the leaves and the soil dug to 10 cm. depth over the area of 1/10 M². After the larger forms were picked out, the material was placed in a Berlese apparatus and the remaining specimens were recovered.

TABLE 2.—Showing the relation of place of collection to number of species and individuals.

Location from Weather Sta.	Conditions	No. of Individuals	Collembola	No. of Species
No. 1. 100 ft. E.	Open space	38	30	12
No. 2. 110 ft. E.	South side of tree; higher and drier than no. 1	97	100	29
No. 3. 732 ft. E. (150 feet from woods' edge)	Heavy leaf cover; lower ground	70	2	18

Three ground collections were made to check variations of populations in different places. The results are shown in Table 2. The discrepancies may be overcome by selecting average leaf cover, canopy, etc., and by multiplying collections.

Scouting and observations were needed to supplement the sweeping and sampling methods as large aggregations were to be found in protected areas; certain species were too swift to be taken in an insect net or in a soil sample; and others massed on certain trees. This fact is especially true in the soil population during the height of the migration which precedes and follows hibernation. General observations were also necessary to determine which species were regular residents in the woods or its edge and the niche they prefer. A close check was kept upon the number of birds and mice in order to determine to what extent they fed upon and disturbed the hibernating, migrating invertebrates.

The Weather and its Effects

RAINFALL AND TEMPERATURE

Weather records were taken in the southeast corner of quadrat N3W2, which is located slightly northwest of the center of the woods. Only the maximum and minimum temperatures recorded for each week were used for comparison with the university weather station. Data used in this paper have been

compiled from the records of the U. S. Weather Bureau Station at the University of Illinois, which is five miles from the woods. A careful comparison of woods data with that of the University Station over a long period showed the two to be quite similar. They were regarded as being sufficiently accurate for the purposes of this discussion.

In a century-long consideration of the abundance of the chinch bug, it was found that deviations from normal temperature and rainfall during their growing season, March through October, and in certain other months, were important. Table 3 shows these deviations for the years under consideration. Table 4 shows other aspects of weather conditions and the status of the vegetation and invertebrates during the period of study.

TABLE 3.—Deviations from normal weather conditions. See Fig. 1.

Year	March through October		Special Months of Rainfall
	Precipitation	Temperature	
1933	—2.37 in.	Above normal	June & July—4.66 in.
1934	—1.64 in.	Above normal	May—3.36 in.
			June+2.02 in.
			June & July+ .96 in.
1935	—1.25 in.	Below normal	May+3.04 in.
			June+0.33 in.
			June & July+1.3 in.

INFLUENCE OF RAINFALL UPON VEGETATION

Since only suggestions are recorded in Table 4 additional statements are necessary.

a. 1933.—This year was much wetter than the year 1934. At least 48 per cent of the rain occurred during the winter and spring; the leaf canopy was more nearly normal. There was a good winter ground cover of leaves.

b. 1934.—The very low rainfall and high temperatures of the early part of 1934 caused herbs such as Geranium, Hydrophyllum, Floerkea, and Asarum to die very early and rapidly so that by June the ground was almost barren. They are commonly 3.5 feet high in June (Table 4).

The pawpaw, the buckeye, and many of the forest trees began to lose their leaves and were almost completely defoliated by August, 1934. While in normal years they are in their height of foliage by this time, three young maples, two oaks, and a buckeye died during this period.

The leaf fall in the autumn showed very definitely the scarcity of precipitation in the hiemal and estival periods. The leaf cover on the ground was only 3 to 4 in. (7-10 cm.) deep and in many places the ground was barren.

The heavier rains and cooler weather of September following the long periods of dry, hot weather in spring and summer caused the herbs and shrubs to make a second growth and by the first light freeze (October 28) many were in bloom and all had an abundant growth of leaves.

c. 1935.—The woods were thoroughly wet for the first time in three years on May 3, 1935. As a result of this large amount of moisture after a dry period a rank growth of vegetation occurred. The herbs were waist high in June. A heavy leaf canopy was formed and no additional trees died during 1935.

INFLUENCE OF RAINFALL AND OTHER WEATHER CONDITIONS ON ANIMAL POPULATIONS

a. *Migration and Hibernation of Species Reproducing Outside of the Woods.*—The effect of rainfall deviations is less immediate in the case of animals than in the case of plants. It has long been known that two or three favorable years are essential to the building up of a large population of chinch bugs (Shelford and Flint, 1943). There are effects on the success of reproduction and development to maturity and also on the longevity of adults as well as the persistence of individuals at points where they may be collected. It is accordingly necessary to consider the origin of the population which may be observed in the cooler parts of the year. First of all it is important to know what species come into the woods for hibernation only and leave in the spring.

Table 4 and Fig. 3 show important facts relative to winter and spring insect movements which bear on the difficulties of securing representative collections on herbs and shrubs. Relatively uniform low temperatures in the winter of 1933-34 held the animals under the leaves until April 1. The above normal temperature of February and March, 1935, tended to make individuals come out of the leaves and many field-inhabiting forms moved toward the woods' edge early.

In a study of the daily maximum and minimum temperatures for these two spring periods, the differences are still more outstanding. Between April 1, and May 8, 1934 (see Table 4, compare 1934 with 1935), there were 30 days with a maximum above 59° F., 14 above 69° F., and 5 above 79° F. These days were so scattered that the invertebrates did not move out of the leaf stratum to any great degree before April 20; after that time the population arose rapidly until it reached a peak on April 24.

During the dry winter of 1933-34 conditions for over-wintering were good: temperatures were relatively uniform and the precipitation was be-

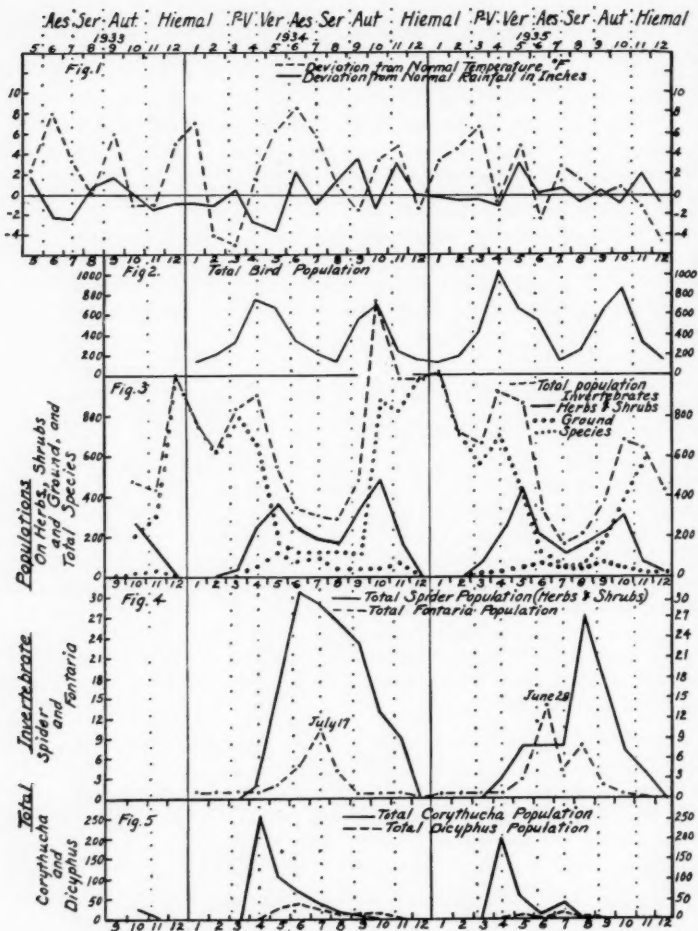


Fig. 1.—Showing deviations from normal temperature and rainfall. Note rainfall November, 1933, to May, 1934.

Fig. 2.—Showing the sum of all birds censused in the forest and forest edge by Twomey. This does not represent the actual population because of probable duplications but is proportional to the actual population; compare with Figure 3.

Fig. 3.—The estimated populations of invertebrates. Attention is called especially to herb and shrub population based on average number of individuals taken in several samples in each month.

Fig. 4.—Showing the populations of spiders and millipeds. Attention is called to

low normal. Insects and spiders were found in considerable abundance in and just under the heavy layer of leaves in the ice crystals and were quite active when disturbed.

The winter of 1934-35 and the autumn which preceded it were characterized by abnormally high rainfall in September and high temperatures

TABLE 4.—Relation of abundance of herb and shrub inhabitants, October 1, 1933, through October, 1935. Summer (Column 4-6) includes the estival, serotinal, and autumnal season (June 1 to October 31). The prevernal period began March 1 and the vernal ended June 11. The hiemal period began November 1 and ended February 28.

SEASON	ANNUAL			SUMMER			VERNAL		HIEMAL		
	NOV. 1 TO OCT. 31			JUNE 1 TO OCT. 31			MARCH 1 TO MAY 31		NOV. 1 TO FEB. 28		
	'33-'34	'34-'35		'33	'34	'35	'34	'35	'33-'34	'34-'35	
COLUMN NUMBER 1	2	3	4	5	6	7	8	9	10	11	
PRECIPITATION IN. (NOTE 1)	28.31	30.3	14.8	20.2	15.7	5.2	12.3	4.0	11.1		
DAYS WITH PRECIPITATION	148	140	48	65	55	35	30	58	55		
DAYS WITH PRECIPITATION MORE THAN .001 (NOTE 2)	101	131	36	50	49	25	41	26	41		
DAYS WITH MAX. TEMPERATURE ABOVE 56°F (NOTE 3)	30	14	8	11	
" 56°F	14	6	2	1	
" 70°F	5	1	1	6	
LEAF COVER (CANOPY)	THIN	THICK	..	THIN	THICK	
HERBS AND SHRUBS	SPARSE	RANK	..	POOR	RANK	..	POOR	RANK	
LEAF COVER (GROUND)	THICK	THIN	GOOD	POOR	
TOTAL OF MO. AVERAGES, INVERTEBRATES PER M ²	1404	1280	..	953	679	329	449	122	152		
HERBS	
PER M ² SHRUBS	782	576	..	443	300	330	276	9	6		
TOTAL BOTH SHRUBS AND HERBS (NOTE 4)	2186	1856	..	1396	979	659	725	131	152		
NUMBER OF SPECIES	245	142	..	180	80	149	50	23	59		

Notes in Table 4.—1. Weather bureau states that a drought starting in June, 1933 was not broken in many localities until September, 1934. Weather bureau reports heavy growth in meadows and pastures in 1935. 2. Heavy snow in February and March, 1934. 3. April 1 through May 8 only, column 7 and 8 only. 4. June through August population on herbs and shrubs—for 1934, 603; for 1935, 479.

TABLE 5.—Showing the relations of number of species and number of individuals to seasons.

1934	Maximum No. of Species for the Entire Month	Maximum No. of Individuals in One Herb-Shrub Collection	Day of Max. Ind.
April	15	199	10th
May	122	594	1st
June	69	314	25th
July	91	277	23rd

the spider maximum in June in 1934 and the late summer decline and the maximum in August in 1935, indicating an increase during the early summer. Note also the larger population of *Fontaria* in 1935 as compared with 1934.

Fig. 5.—Showing the population of two species of Hemiptera. Attention is called to the small population of both species, in 1935.

in October and November. The field-inhabiting forms came into the woods early and remained on the vegetation. Large aggregations of *Bibio* larvae (March flies) were found in various parts of the woods. The larger invertebrates were scarce. From December 12, 1934, to January 6, 1935, the ground was covered with snow; by January 9, the maximum and minimum temperatures were 52° F. and 45° F., respectively, and 0.95 inches of rain occurred within two days. Nabids, millipeds, spiders, pentatomids, coreids, chinch bugs, *Thysanura* and *Collembola* were crawling on tree trunks, roots, logs, and leaf surfaces avoiding the slush and water.

The whole winter of 1934-35 was characterized by alternating extremes of cold and warm periods accompanied by snows and rains. These extremes appeared to be serious to many of the insects caught too near the surface at various stations.

In February a warm rain was followed by several days of zero weather. A group of chinch bugs and lady beetles (*Ceratomegilla*) were brought to the laboratory and thawed out. One out of every five chinch bugs and two out of every five *Ceratomegilla* died. A check in the field showed about the same mortality rate. From the field and laboratory observation it appeared that insects were much more resistant to sudden radical changes of heat and cold during the early winter than later in the winter and early spring.

The number of species appearing in the collections in any month differs in the two years (See Fig. 3). The usual variations related to the migrations of hibernating forms are shown in Table 5. Variation in the size of

TABLE 6.—Dates of maximum individuals on herbs and shrubs due to movement associated with hibernation.

Observer	Year	Spring		Autumn	
		First	Second	First	Second
Weese	1921	—	—	Sept. 26	Oct. 8
Weese	1922	May 1	May 8	—	—
Blake	1924	Apr. 24*	—	—	—
Rice	1933	—	—	Oct. 5	—
Rice	1934	Mar. 15	Apr. 10 & May 1	Oct. 3	Oct. 22
Rice and Kanatzar	—	Mar. 20	May 21	Sept. 17	Oct. 29

* Approximate

the populations is a general cause of variation in the number of species collected in the random sampling. The number of samples is small because of the difficulty of analyzing them. The less abundant species may be missed entirely and the greater the number of species with sparse population, the more will be missed. This applies to both resident species and those migrating into the forest from the forest edge in the autumn and out again to surrounding cultivated fields in the spring. However, a very important factor is the variation in the time at which the migrants enter and leave and the number of species that do so.

In 1934 the mean daily temperature began to rise in the middle of March and the last snow melted on March 29. By April 2 the temperature reached 70° F.; as a result invertebrates began to come up out of the leaf stratum and on the 10th the number of species was the highest of the month.

On May 1 representatives of both the hibernation migrants and the perennial species were present, giving a maximum of species in spite of the fact that most of the migratory population had moved out. The large num-

TABLE 7.—Showing the relative abundance of herb and shrub inhabitants in 1934 and 1935 in comparison with the ground inhabiting *Fontaria*. Figures in columns 3, 4, 5, and 6 are estimated number of individuals per square meter. Column 1 compares the populations for the two years in terms of percentage of 1934. Column 2 refers to graphs showing relative abundance. Columns 3 to 6 compare the populations in the same months in different years. The designation "1st" in the column 3 refers to the first month in which the species indicated became prominent. This ranged from April to June, depending on the species.

Column numbers	1	2	3	4	5	6
	% 1934	See Fig. No.	1st month		August	
			1934	1935	1934	1935
August	89				176	157
June through October	71					
June, July and August	79					
Spiders	63	4	18	8	26	27
Corythucha	50	5	255	200	13	6
Dicyphus	45	5	29	2	11	7
Gargaphia	45		12	6	6	5
Fontaria	137	4				

TABLE 8.—Invertebrates, seeds, and fruits destroyed by each of fifteen common species of birds in the forest and its margins chiefly in 1935. The insect groups which predominated, are indicated by orders; the seeds and fruits and other invertebrates are not separated. Barred owl pellets were also analyzed. Thirty of these showed the following identifiable fragments: Vernal period, (March 1-June 1) 85% mice; Aestival period (June 1-Sept. 1) 75% mice, 10% birds; Autumnal period (Sept. 1-Nov. 1) 90% mice and shrews; Hiemal period (Nov. 1-Mar. 1) 95% mice and shrews. (Collection and identification of birds by C. C. Towney).

[illegible]

ber of individuals of June 25 was maintained after the migrants had all left by the appearance of nymphs of Hemiptera, especially of lace bugs.

The dry warm spring did not make as much difference in the number of individuals as in the number of species (Table 4): 149 in 1934 and 50 in 1935. Throughout the whole period from Nov. 1, 1933, to Oct. 31, 1935, there was less difference in the total number of individuals than in species. There were around 2,187 individuals, representing 245 species listed for 1934 and 1,724 individuals, representing 142 species for 1935.

The dates of maximum abundance due to the movements of forms which migrate into the woods for hibernation and out of the leaves onto the herbs and shrubs and thence to the forest edge and fields are suggested in Table 6. As will be seen the dates of the first maxima in spring have varied 45 days and 18 days in autumn in correlation with temperature and rainfall conditions.

b. Variations in Population of Resident Species Reproducing in the Woods.—Since the species which reproduce in the forest edge, grassland, and cultivated fields may not respond in the same way as the forest residents, attention should be given to resident species. The following resident forms were more abundant in both species and individuals in 1934 than in 1935: Pentatomidae, spiders, Hymenoptera (especially the parasitic types), leaf hoppers, and all Hemiptera. In 1935 the following were more abundant than in 1934: miscellaneous Diptera, crane flies, snails, aphids, chermids, Phylloxera and other Homoptera. Slugs, both *Deroceras gracile* Raf. and *Philomycus carolinianus* (Bocsi) were abundant—13 were taken on one tree trunk 5.5 feet from the ground on August 8; none was taken in 1934.

The large number of individuals both years was due to tingids (*Corythucha*) (Fig. 5) a flea beetle (*Glyptina*), the striped cucumber beetle (*Diabrotica vittata* Fabr.), the basswood beetle (*Baliosus*) and two species of snout beetles found in *Floerkia* and *Geranium*. The large summer population in 1934 was due to a mirid (*Dicyphus gracilentus* Par.) (Fig. 5) which had a large generation in May and June, and to stiltbugs (*Jalysus spinosus* Say), spiders, and leaf-hoppers.

Blake (1931) checked the animals listed as of ecological importance by Weese and Smith over this same elm-maple forest and listed 35 properly identified species of invertebrates as being of sufficient importance to merit particular mention. In 1934 and 1935, 30 of these species occurred on two of the three lists (Weese, Smith, Blake), and 4 were common to all three. These four are two spiders, *Pityohyphantes costatus* (Hentz) (syn. *Linyphia phrygiana* (Koch.)) and *Ayscha gracilis* (Hentz) (syn. *Anyphaena rubra* Em.), a coccinellid beetle (*Telephanus velox* Hald.) and a chrysomelid beetle (*Phyllotreta sinuata* Steph.). Weese did not give specific reports on the ground inhabitants and Blake did not work through the summer. There were doubtless other elements of choice of species to illustrate their conclusions. However, the following were common to two of the three lists and to the findings of the writer: Chrysomelids (*Diabrotica vittata* Fabr., *Epitrix fuscata* Cr., *E. brevis* Sz. and *Glyptina spuria* Lec.), two leafhoppers

(*Empoasca viridescens* Walsh and *Erythroneura obliqua* Say), one lace bug (*Corythucha aesculi* O. & D.), and a spider, *Dictyna foliacea* Hentz (syn. *D. volupis* Keys.). The variations in abundance of several species in the two summers (1934-35) are stated below:

Yellow-margined Millipede, *Fontaria virginiensis* (Drury) (Fig. 4).—Weese mentioned this species in his August 1922 collections; Blake named a society for it because it appeared in his fall and winter collections; Smith-Davidson lists it as a common form. As will be seen by Figure 4 this form was very conspicuous July 17, 1934, when a breeding swarm reached its peak following some light showers. A few specimens were seen from the middle of May to the middle of August. At that time the millipeds crawled well under the leaves, due probably to a moisture relationship. In 1935 they became rather abundant around May 24, occurring under leaves near the bases of trees or shrubs, and reached the peak of abundance as a mating swarm on June 28, following a period of high humidity. They gradually diminished in numbers during the month until only one or two were seen under leaves and boards during September. Four adults brought into the laboratory in November 1933, laid eggs, which hatched January 20 to 25 at room temperatures.

Buckeye Lace Bug, *Corythucha aesculi* O. and D. (Fig. 5).—In 1934 this species reached a peak of abundance on April 24 and was mating May 1. Many patches of eggs were seen on buckeye trees on May 8 and 15; the first young were seen May 22 and practically all had hatched by May 31. In 1935 there was a large number in late April emerging from hibernation, but the later population was much smaller.

Basswood Lace Bug, *Gargaphia tiliae* (Walsh).—In 1934 this appeared on the basswoods in great abundance on May 8; the first nymphs appeared May 31 and reached a peak June 5. The 1935 population was very small throughout the summer.

Rounded-shouldered Stink Bug, *Menecles insertus* (Say).—This bug was listed by Weese as occurring from May until August. In 1933 they were abundant all winter in the fallen leaves and were numerous on the surface during April and May, 1934. At the beginning of June the young began to appear in great numbers. Both adults and nymphs were extremely abundant all summer. By September 19, they were hiding under the leaves and were not seen unless one searched for them. They made their appearance April 3, 1935, and were seen occasionally during the summer, but only in small numbers as compared with 1934.

Basswood Beetle, *Baliosus ruber* (Web.).—In 1934 this beetle became very abundant by May 8 and was at its maximum May 15. It remained in the woods all summer with average collections of 8 per square meter. In 1935 it appeared first on April 24. Its peak was reached in June, with average collections of 8 per square meter; collections of 4 per square meter were average for the summer.

Cucumber Beetle, *Diabrotica vittata* Fabr.—In 1934 this beetle reached its greatest abundance May 1 and continued relatively abundant until after May 31. In 1935 its greatest abundance was on April 24 (see Weese, 1924) but it was only about one-twentieth as numerous as in 1934.

Leaf-legged Bug, *Acanthocephala terminalis* (Dall.).—In 1935 only adults were taken May 8 through July 23. In 1935 only nymphs were taken in August at an average of 5 per square meter.

The Plant Bug, *Dicyphus gracilentus* Par. (Fig. 5).—The peak of abundance in 1934 came in June and they remained abundant throughout the summer. In 1935, there were few in spring and the peak came in July.

Snails which were listed as important in the work of Weese, Smith, and Blake, were missing almost entirely in 1934 and just beginning to come back in 1935 collections. The Weather Bureau refers to "The drought which had its beginning in June 1933, was not definitely terminated for the state as a whole until September 1934." In the area of study, however, there was some relief in June 1934, when rainfall was 2.02 inches above normal.

An examination of Figures 1 to 5 taken with Table 4, etc., shows that the inhabitants of the herbs, shrubs, and young trees were more abundant in a summer with rainfall below normal and plants suffering from lack of water. This applied to several species and to the total herb and shrub spider population. On the other hand the ground-inhabiting species showed greater populations in the moister summer. Since the total monthly average populations on the herbs and shrubs for the period November through October included the migrating insects, the period June through October was used to eliminate those individuals belonging to the preceding year which usually have left the woods by June (see columns 5 and 6, Table 4; and Table 7). The 1935 population for June through October was only 75 per cent of the 1934 population for the same period; whereas, the total population for 1935 was 85 per cent of that for 1934. The June through August total for 1935 was 79 per cent of that for 1934 (see footnote 4, Table 4; and Table 7).

The reduced number of plant-inhabiting species in the summer with much vegetation is not easily explained. More years of observation will be necessary to establish the causes. The size of the population over-wintering in the favorable winter of 1933-34 is possibly responsible. Table 7 shows evidence of such a relation. Each species separated as a different population shows larger populations in the month in which herbs began to be prominent in the year of 1934 as compared with 1935 (columns 3 and 4). The graphs of all these species show a smaller, i. e., a declining population toward the end of the summer of 1934 and an increase toward the end of 1935. This appears to correlate with the rainfall (Fig. 1).

Relation of Population of Invertebrates to Other Organisms

Table 8 gives a list of bird stomach contents determined by the author (birds collected by A. C. Twomey). From this table one can easily see that the principal food throughout the year is insects. Since these birds are either year-round or summer residents, one meal or feeding gives some idea of the effect they must have upon the invertebrate population of the woods. The stomach contents represents one day's feeding.

Twomey lists 73 nesting pairs and 146 individuals for 1934 and 62 pairs and 124 individuals in 1935. The birds are fed for about two weeks and feed in the woods for from two to four weeks more. While in general about half of the young birds are destroyed through the destruction of nests or otherwise, nests are rebuilt and the process started over again; about half of the species listed in Table 8 raise a second brood which covers another month while most of the young birds of the first brood are still in the woods. Accordingly, without exact information in any of the fields, the young may be considered as continuing to reduce the insect population for a total of 60 days (June 1 to July 31).

As an example of the frequent use of insects as food, Twomey states that in 1934 there were five downy woodpecker nests well distributed over the woods. The young hatched in early June and were fed every 3.5 minutes. The food was taken within 150 meters of the nest. The feeding day, in June and July, averages nearly 15 hours. This means that the birds of each nest would be fed about 250 times or each of the four birds would be fed about 60 times per day. This calls for 240 larval or adult insects of the larger types, such as lepidopterous larvae, Orthoptera, large Hemiptera, etc., per nest each day. For the 73 nests for 60 days, 1,051,200 large insects were needed to feed the young in 1934.

As to the 146 adults: in general, birds are known to take seven meals per day. The 105 stomachs examined contained an average of 39 insects, representing one meal. Each of the 146 birds, representing two per nest, would take 273 insects per day or a total of 39,858 insects per day to feed the adult birds or for the 60 days, 2,391,480; this added to the 1,051,200 required to feed the young makes a demand of 3,442,480 insects.

On May 31, 1934, there were about 350 insects and spiders on the herbs and shrubs of each square meter, or about 70,000,000 food animals in the entire 20 hectare area. This was 20 times the food consumed daily, chiefly from the herbs and shrubs. Most of the insects of the first or of the second generation had appeared as nymphs or larvae, while many with different life histories were present as adults. This population declined to approximately 47,800,000 for the average of June, to 37,600,000 for the average of July, and to 25,200,000 on July 30, while there was still further decline in the average for August. As shown by Table 8 the food used by the adults during that aestival period when most of the feeding of young is going on, consists chiefly of Lepidoptera, Diptera, Hymenoptera (sawflies, etc.) and large palatable Hemiptera.

It is well known that birds tend to feed their young a larger proportion of insects than they use themselves. A decline or failure to increase must necessarily follow from the constant picking off of a selected group of individuals belonging to the orders named and cannot fail to have an important effect, especially when weather conditions are unfavorable as was the case in 1934. Further, this predation may be the fundamental cause of generally small summer populations of the groups involved. The small species, such as leafhoppers and fleabeetles, are very little affected by bird predation and with further study may be used as indicators of weather effect, which will make possible better evaluation of the separate action of birds independent of weather. In 1935 there was a decline of insects from the end of May until after mid-August when an increase began.

As has been shown by Weese (1924) and Smith-Davidson (1928, 1830), insects move into the forest interior from adjoining fields, grasslands, and forest edges onto the herbs and shrubs in large numbers mainly in October. Residents come down from the tree tops about the same time; hence the number of individuals on the herbs and shrubs is larger in October or early November. The exact time is dependent on autumn weather conditions, especially temperature. This may be noted in Figure 3. The high point came in October 1933 and 1934 and October in 1935. The maximum collections occurred as follows: 1933, October 5; 1934, September 29 and October 3; 1935, October 29. The increase began about mid-September in 1934 and 1935. The bird migration population reached its maximum about October 1, 1934, and in mid-October 1935.

In the spring of 1935 the maximum of both forest insects and migrating birds came at the end of April, a little earlier than in 1934 when the temperatures were lower (see Fig. 2). Since both birds and insects are influenced by temperature, they vary from year to year in a similar manner.

In winter the invertebrates are almost entirely confined to the leaf cover and soil. The drop in ground population in mid-winter is due to the retreat of many species which occupy the soil at all times to depths below the surface (see Fig. 3), but when they again return to the surface the total population is smaller, probably chiefly due to mortality of the forms hibernating in the leaves.

About January 20, in both 1934 and 1935, a large flock of robins, between 250 and 300 birds, appeared in the south end of the woods and remained until early March. They thoroughly overturned the leaves throughout the southern half of the woods, and in 1935 eliminated eight large aggregations of bibio larvae (*Bibio albipennis* Say), so that 3 weeks later no bibio larvae were to be found in that area though one or two small aggregations were left in the northern half. The stomach contents of 12 birds averaged 40 larvae, 4 beetles and 13 Hemiptera each. The most larvae found in one stomach was 128. In three weeks 250 robins probably consumed approximately 200,000 larvae, 21,000 beetles and 66,250 Hemiptera.

A soil and leaf sample was taken from the area worked over by the robins and another from the northern section of the woods, March 17, 1935. One square meter in the undisturbed area gave 1,914 individuals—Diptera, spiders, flea beetles, earthworms, *Notoxus* and *Thysanura*. The area worked by robins gave 300 forms, principally *Thysanura* and chinch bugs, 1 spider, 1 negro bug, *Notoxus* and 2 pentatomids. The birds had consumed about five-sixths of the invertebrate population in the leaves.

The dead maples referred to earlier gave boring horn-tail larvae a large opportunity. In 1934 they were evidently numerous on June 25. As many as 15 of their parasite, *Meyarhyssa* sp. (probably *lunator*) were found on one tree. Some could not loosen their long ovipositors and died in position on the tree trunks. The short dry vegetation of 1934 did not encourage as large broods of aphids and ants as in 1935. Also there were not as many leaves to eat and there were fewer larvae. Even the numbers of moths laying eggs were less noticeable in 1934.

Summary

1. Sweeping a definite area showed that 50 strokes would give an average sample of inhabitants of that area but would not take all individuals on the area.
2. The population of resident species inhabiting the herbs and shrubs was larger in 1934 than in 1935. The over-wintering population of these species was much larger in the spring of 1934 than in the spring of 1935.
3. The population of certain herb-inhabiting species declined during the summer of 1934, in which rainfall was below normal in May. The population increased toward the end of the summer of 1935 in which rainfall was much above normal in May and slightly so in June and July.
4. The winter and migrant population of birds ranges from 400 to 600 and is 70 per cent insectivorous. In 1935 robins took five-sixths of the hibernating invertebrates in an area of ten hectares.
5. The largest number of migrating birds came through when the insect population was moving in and out of the woods for hibernation.
6. While the population of invertebrates available to birds is probably 20 times that consumed by birds, including young, the pressure falls on the Lepidoptera, Diptera, Hymenoptera (sawflies, etc.) and large palatable Hemiptera while the small leafhoppers and fleabeetles are utilized to a small extent. The species with large individuals are rarely abundant in the woods.

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MANGUM HIGH SCHOOL,
MANGUM, OKLAHOMA.

Variations in Abundance of Certain Invertebrates in William Trelease Woods, 1933-1938

Sarah E. Jones

This paper differs from several others on the same area in that it proved possible to trace variations in abundance (annuation) for five consecutive years for several species and for four years for a larger number. Some effort was made to trace changes from season to season (aspection) and some results were worthy of record. The difficulties encountered made possible a statement of the best methods to follow.

Several community studies have been made at the University of Illinois, largely in the two woodlands owned by the University and known as William Trelease Woods (formerly University Woods) and Brownfield Woods. McDougall (1922) has given an account of the plants in William Trelease Woods, and in 1928 he and Penfound made a further report upon the plant forms there. Weese (1924) studied the invertebrates in this woodland during 1921-1922. Several later workers have considered various phases of the community problem. Blake (1926) gave an account of hibernation among invertebrates, based on his observations made during the winter of 1924-1925. In a later paper (1931) he considered the spring population of 1925. Rutherford (1929), working in Brownfield Woods, studied the movements of insects in hibernation. Smith-Davidson (1930) reported upon the tree-layer society in both Brownfield and William Trelease Woods, a phase heretofore neglected. Her later paper (1932) gave an excellent account of seasonal variability and its effect upon total populations as seen in 1925-1926.

In 1933 studies of the animal community at William Trelease Woods were begun in the desire to have continuous records of animal populations over a period long enough to indicate the reactions of the animals to weather changes. Collections of invertebrates from 1933 to 1935 were made by Rice (1944) and were continued from 1935 to 1936 by Kanatzar, who prepared a master's thesis which was not published. The writer's work began in the fall of 1936 and continued until September, 1938. Rice (1946) tested the methods used and analyzed the populations of forest species with reference to weather and bird predation. Her work began October 1, 1934, and ended with September, 1935. However, she made use of Kanatzar's data through November, 1935, and began her most serious analysis with November 1, 1933, and ended with October 31, 1935.

It was possible for the writer to report on nine species through the entire period, on six species through Kanatzar's period of study, and two species through Rice's period of study with Kanatzar's year omitted. Only one species analyzed by Rice was graphed by the author and this for a different purpose.

Description of the Habitat

William Trelease Woods is a 50-acre tract of woodland located five miles northeast of Urbana. It is bordered on three sides by cultivated fields and on the west by a road.

The woods is an undisturbed woodland as regards shade and canopy though a few trees were removed about 50 years ago. There has been very little disturbance since the University of Illinois purchased the land in 1918. The forest is gently rolling, with the 690- and 700- foot contour lines passing through it. The greatest difference in levels probably does not exceed sixteen feet. The soil is yellow-gray silt loam characteristic of upland forests. The drainage is poor, so that in wet seasons water may stand in the lower parts of the woodland for several weeks. This commonly happens in the spring, and to a lesser extent in the fall. The low ground is never very dry. Associated with the difference in soil level and the corresponding difference in moisture there is a difference in tree species: thus elm (*Ulmus americana* Linnaeus and *U. fulva* Michaux) is dominant in the lower regions; whereas sugar maple (*Acer saccharum* Marshall) is dominant in the higher parts. In the locality where collections were made elm is more abundant than maple. William Trelease Woods may be considered in part a climax forest since sugar maple is a characteristic climax tree for the region.

McDougall (1922) gave an account of the plants present in William Trelease Woods. Maple and elm are the dominant trees, with American ash (*Fraxinus americana* Linnaeus), blue ash (*F. quadrangulata* Michaux), basswood (*Tilia americana* Linnaeus), and blue beech (*Carpinus caroliniana* Walter) next in abundance. The shrub layer, in addition to saplings, is made up of two common forms, papaw (*Asimina triloba* Dunal.) and spice bush (*Lindera benzoin* (L.) Blume).

The herbs are divisible into two layers. The tall herbs are composed primarily of nettle (*Laportea canadensis* (Linnaeus) Gaud.) and touch-me-nots (*Impatiens pallida* Nuttall and *I. biflora* Walter), both of which are very abundant in the summer. Lower herbs characterize the vernal season and consist largely of trillium (*Trillium recurvatum* Beck), Dutchman's breeches (*Dicentra cucullaria* (Linnaeus) Millsp.), spring beauty (*Claytonia virginica* Linnaeus), false rue anemone (*Isopyrum biternatum* (Raffinesque) Torrey and Gray), blue-eyed Mary (*Collinsia verna* Nuttall), blue phlox (*Phlox divaricata* Linnaeus), wild geranium (*Geranium maculatum* Linnaeus), and blue violet (*Viola sororia* Willdenow). Many of these disappear early, while wild ginger (*Asarum canadense* Linnaeus) and waterleaf (*Hydrophyllum appendiculatum* Michaux and *H. canadense* Linnaeus) become evident a little later than the others. May apple (*Podophyllum peltatum* Linnaeus) blooms late in the vernal season but, as in the case of many herbs, the plants remain green until the following fall.

The forest floor is covered by a heavy litter. In the autumn dead leaves form a dense cover and these together with fallen twigs and branches slowly decay as the season advances.

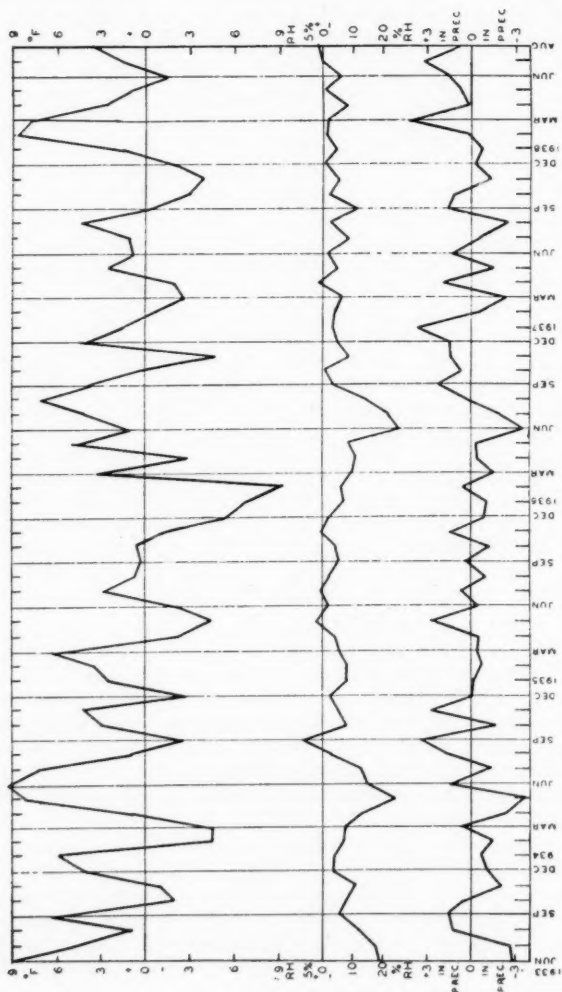


Fig. 1. Deviations of temperature (above), relative humidity (center), and precipitation (below) in 1933-1938 from the average of forty years in Urbana, Illinois. Temperature in degrees Fahrenheit; relative humidity in per cent; and precipitation in inches.

As has been stated above, William Trelease Woods has suffered very little interference since 1918. However, before this time all the larger mammals (deer, bear, fox, etc.) had been eliminated. This extirpation is one important factor causing the woodland to differ from its original condition, and the effect of the surrounding cultivated land is another. As Rutherford (1929) points out, there is movement of the smaller prairie animals back and forth between woods and field. Also, animals foreign to an Illinois forest, such as cats, dogs, and occasional stray chickens, have been introduced because of cultivation and nearby farm homes.

Methods of Study

Only the invertebrates in the woods have been considered by the writer. From September, 1936, to September, 1938, weekly collections were made. These collections included forty-eight sweeps of the shrubs and of the herbs; these were made with an insect net thirty inches in diameter. This unit was regarded as giving the population of one square meter. Rice used fifty strokes for the area. No correction was made for the incompleteness of shrub ground-cover. The animals were etherized, brought into the laboratory, and sorted. Soil samples were made with the use of a tenth-meter iron ring, and animals were sorted in the field and either etherized or placed in alcohol. The numbers derived from these samples were multiplied by ten to represent the number in one square meter (the unit used in herb and shrub collections). The specimens were sent to various specialists for identification.

Weather Data

Instruments located at the point where collections were made in William Trelease Woods provided much of the data upon which the weather reports are based. These instruments include an air hygrothermograph, maximum and minimum thermometers, a soil thermograph, and two rain gauges. This equipment was checked once a week, and the records obtained were supplemented by those from the United States Weather Bureau located on the University of Illinois campus.

The weather conditions for 1933-1938, as compared with the average ones over 40 years in Urbana, are shown in Figure 1.

Invertebrate Populations

The appearance of the woods varies from one season to another and from one year to another. The annual cycle has been arbitrarily divided into six seasons whose limits are not clearly defined but which have general differences. These seasonal changes are known as aspection. Each season has characteristic climatic conditions, vegetation, and animal activity. These

seasons, their limits, and a generalized account of activity in each are given below. The description does not apply strictly to any one year, but is a combination of the conditions noted in several years.

Season	Time	Indicators
Hiemal	Nov. 1 to Feb. 28	Hibernation of most invertebrates
Prevernal	March 1 to April 14	Activity of Lycosidae and Thomisidae on the ground
Vernal	April 15 to May 31	Movement of many animals into herbs and shrubs; migration of seasonal species
Estival	June 1 to July 14	Appearance of many flies; movement of many flies and ants into the upper layers
Serotinal	July 15 to Aug. 31	Appearance of young of many spiders and mirids, with decrease in numbers of adults of these species
Autumnal	Sept. 1 to Oct. 31	Migration of seasonal species into the woods and down to the soil; disappearance of flies and other summer animals

The hiemal season is characterized by low temperature, low precipitation, and high humidity. The plants are in a resting stage, and the animals are in hibernation. The majority of the invertebrates are on the ground or in logs; many of these remain quiescent throughout the hiemal season, but others become active on warm days. Soil inhabitants include millipedes, centipedes, many spiders (*Xysticus* spp., *Anyphaena pectorosa* L. Koch, *Erigone* spp., *Allocosa* spp., and *Dictyna foliacea* (Hentz)), snails (*Vertigo ventricosa* (Morse), *Carychium exile* H. C. Lea, *Succinea avara* Say, and *Retinella indentata* (Say)), adult beetles (*Hypera punctata* Fabr., *Phyllotreta sinuata* Steph., *Notoxus* spp., *Mycetoporus* sp., *Lathrobium* sp., *Diabrotica* spp., *Phalacrus politus* Melsh, *Epitrix* spp., and *Philonthus* spp.) and other groups. Larvae of many beetles and flies are in the soil. Some forms, such as *Myodocha serripes* Olivier, *Lygus oblineatus* (Say), *Tetragnatha laboriosa* (Hentz), and *Neoscona benjamina* (Walck.), may remain among the herbs and become active in favorable weather.

The daily temperature range increases in the prevernal season as the temperature rises. There is much precipitation, but the relative humidity drops. The majority of the animals, though more active than in the hiemal season, remain on the ground. *Anyphaena pectorosa* and *Tmarus angulatus* (Walck.) are among the first animals to move into the herbs. On the ground young Lycosidae and Thomisidae are conspicuous while animals such as *Epitrix brevis* Schwarz which have hibernated deep in the soil move up to the surface.

During the vernal season there is a great increase in activity. Temperature is much higher, plants develop leaves, and the spring herbs appear in profusion. Associated with the development of the plants is the migration

of many invertebrates. *Epitrix brevis*, *E. fuscata* Crotch, *Lygus oblineatus*, *Blissus leucopterus* (Say) and other insects move into the herbs and shrubs and leave the woods for the forest edge or open field; this migration usually extends into the estival season. Typical herb inhabitants move into this layer from the ground, and soil inhabitants conspicuous in the summer may become active in the vernal season. Ants are important in the latter group. The vernal season has some characteristic animals seldom seen in other periods; *Idiostethus subcalvus* Lec. and the adult of *Malthodes spado* Lec. are examples. Many leafhoppers which are seen in this season are seldom seen again until the late serotinal or autumnal season.

In the estival or early summer period the temperature continues to rise and the relative humidity continues to drop. Precipitation is usually not as great as in the spring. The spring herbs disappear and the forest assumes its characteristic summer appearance, with heavy foliage. Migratory insects soon disappear, and the permanent residents of the woods are more in evidence. Snails and slugs move between the ground and herbs, and flies, especially Tipulidae, are abundant, while spiders such as *Araneus marmoreus* Clerck, *Micrathena gracilis* (Walckenaer), *Dictyna foliacea* (Hentz) *Tetragnatha extensa* (Linnaeus), and *Agelena naevia* Walckenaer form many webs. Other wandering spiders live among the herbs, shrubs, and ground litter, and nymphs and other young stages of animals which reproduce in the vernal season are present in great abundance. The adult of *Cantharis* sp. is a characteristic animal seldom seen in other seasons.

The serotinal season, in the second half of the summer, is not sharply distinguished from the estival season. The temperature reaches a maximum and relative humidity is at its minimum. Many Compositae are in bloom, but otherwise the vegetation is much as it was during the estival season. There are no characteristic animals, but the numbers of the species present in the estival season may be changed. Immature invertebrates are abundant, as in the estival season, and new forms are added to the list of these because of reproduction of several forms in the estival season.

The conditions of the autumn season are the reverse of those in the prevernal and vernal seasons. The temperature gradually falls, and its daily range is great. Both relative humidity and precipitation are greater than in the summer. Trees and shrubs lose their foliage and many herbs die, so that the ground is covered with a thick layer of decaying matter. The animals which spent the summer on the forest edge or in the fields now migrate into the woods for hibernation, first coming into the herb and shrub levels and then moving down to the soil. Mature leafhoppers, chrysomelids, and Neuroptera are now more abundant than at any other time of the year. Herb and shrub inhabitants move to the ground for hibernation and at the close of the autumnal season the forest is bare and quiet for another winter.

General considerations upon invertebrate populations will be better understood after a survey of some of the more important species. Therefore accounts of the annuation, or changes from one year to another, of different species are given here first.

Species, Habitat, Aspection, and Annuation

- Retinella indentata* (Say), snail. Fig. 2.—In soil; few in summer; adults in winter. Probably helped by moist summers.
- Meracantha contracta* (Beauv.), darkling beetle. Fig. 2.—Larvae in logs and dead twigs on ground. Reproduction probably in spring. Increased with increasing summer humidity in 1937 and 1938.
- Allocosa funerea* (Hentz), wolf spider. Fig. 2.—On ground, conspicuous in prevernal season. Probably reproduces in summer. Moist summers possibly helpful.
- Scytonotus granulatus* Say, millipede. Fig. 2.—Mostly in soil, with maximum in summer. More abundant in 1937 and 1938 than in 1936. Summer humidity probably helpful.
- Phidippus* spp. jumping spider. Fig. 2.—Wanders among shrubs; reproduces in estival season. Numbers increased or fell in 1933-1938 as estival humidity rose or dropped.
- Tetragnatha extensa* (Linn.), orb-weaver. Fig. 2.—Abundant in herbs and shrubs; reproduces in June. Far more numerous in 1938 than in 1937 or 1936. Moist estival season probably helpful.
- Allocoris* (*Corimelaena*) *pulicaria* (Germ.), negro-bug. Fig. 2.—A migrant, going to forest edge in the summer, when it reproduces. Possibly favored by moist estival season. Most abundant in fall of 1935.
- Succinea avara* Say, snail. Fig. 3.—In herbs, most abundant in fall and spring; possibly helped by late summer moisture.
- Carychium exile* H. C. Lea, snail. Fig. 3.—In soil; least abundant in spring. Probably favored by cool, moist summers.
- Gargaphia tiliae* (Walsh), lacebug. Fig. 3.—(Upper curve shows nymphs; lower one, adults.) In herbs and shrubs; most abundant in summer, when reproduction probably occurs. Evidently helped by cool and moist summers, and injured by severe winter of 1935-1936.
- Chauliognathus pennsylvanicus* (DeGeer), soldier beetle. Fig. 3.—Larvae in soil in winter and spring; adults in herbs in estival season. Far more abundant in 1937-1938 than 1936. Cool, moist summers probably favorable.
- Ptilodactyla serricollis* (Say), soft-bodied plant beetle. Fig. 3.—Larvae in soil; seen least in midsummer, when reproduction probably occurs. Increased in 1937 and 1938. Low temperature and high relative humidity in summer probably helpful.
- Vertigo ventricosa* (Morse), snail. Fig. 3.—Eggs probably in June; in soil in dry weather, on herbs in damp weather. Probably aided by vernal and estival moisture.
- Deroceras agreste* (Linnaeus) (*Agriolimax agrestis* (Linn.)), snail. Fig. 3.—Mostly in soil, from May through the autumn. Probably favored by vernal and summer moisture.
- Deroceras gracile* Rafinesque (*Agriolimax campestris* Binney), snail. Fig. 4.—Like *D. agreste*, but more abundant. Very active on rainy days; probably favored by vernal and summer moisture.
- Epitrix brevis* Schwarz, flea-beetle. Fig. 4.—Migratory, spending summer on forest edge or in field and hibernating deep in forest soil; seen most in herbs and shrubs in spring and fall. Perhaps secondarily dependent upon moisture, which affects food plants. Scarce following dry summer of 1936, and apparently injured by severe winter of 1935-1936.
- Ponera coarctata pennsylvanica* (Buckley), ant. Fig. 4.—In twigs on ground; rare in winter. Colonial, and thus difficult to evaluate. Increased from 1936 to 1938; presumably aided by spring and summer moisture.

- Dichomeris ligulella* Hbn., palmer moth. Fig. 4.—Adults seen mostly in serotinal season, clustered around Compositae. Far more seen in 1938 than in the two preceding years. Rising spring and summer humidity may be helpful.
- Polygyra thyroideus* (Say), snail. Fig. 4.—Eggs early vernal; in herbs from late May through summer. Probably favored by vernal rains. Scarce following the dry winter and spring of 1936.
- Erigone* spp., sheet-web weaver. Fig. 4.—Hibernate in soil; in herbs in spring and summer; probably reproduce in vernal and estival seasons. Increased with increasing spring and summer humidity and decreasing spring and summer temperature from 1936 to 1938.
- Chrysopa plorabunda* Fitch, lace-wing. Fig. 4.—Adults among herbs and shrubs in late fall; reproduction probably in spring. Apparently cool, humid vernal and summer seasons helpful.
- Philonthus* sp., rove-beetle. Fig. 4.—In soil, most numerous in spring and summer. More abundant in 1938 than in 1937. Warm moist spring possibly beneficial.
- Chalepus nervosa* Panz, wedge beetle. Fig. 2.—Adults hibernate in soil; in herbs in summer. Least seen in 1938. High summer humidity not favorable.
- Mycetoporus* sp., rove-beetle. Fig. 2.—A soil resident; more abundant in 1937 than in 1936 or 1938. Importance of weather doubtful, though excessive humidity may be harmful.
- Dicypus gracilentus* Parsh., leaf-bug. Fig. 2.—In herbs and shrubs from late vernal through autumn season. Reproduction in early summer. Greatest numbers in 1934 and 1936, which had hot and dry summers.
- Apion griseon* Smith, weevil. Fig. 2.—Adults hibernate and go to waterleaf in vernal season; scarce in midsummer, when reproduction probably occurs. Most abundant following summers of 1933 and 1936, which were hot and dry.
- Diclyna foliacea* (Hentz), spider. Fig. 2.—In herbs and shrubs; reproduction in estival season. Juveniles hibernate. Most abundant in 1936, less in 1937. Warm, dry summers beneficial.
- Xysticus* spp., crab spiders. Fig. 2.—Reproduction probably in vernal and estival seasons; on ground and among herbs and shrubs; greatest numbers in spring of 1934, less in 1937. Cold winter of 1935-1936 possibly harmful.
- Notolus monodon* Fabr., ant-like flower beetle. Fig. 2.—Seasonal, hibernating in forest soil; reproduction in summer. Most abundant in winter of 1936-1937, next in winter of 1933-1934. Hot summers favorable.
- Chalepus rubra* Weber, wedge beetle. Fig. 3.—Like *C. nervosa* but less abundant and primarily in soil. Reproduction probably in estival season. Greatest numbers after hot summer of 1933; cold winter of 1935-1936 probably harmful.
- Epuraca rufa* Say, sap-feeding beetle. Fig. 3.—In soil, least abundant in early spring and late summer. Reproduction probably in vernal season; far more abundant in vernal season of 1937 than in 1938; these were produced in 1936, when the spring and summer were hot and dry.
- Dendryphantes capitatus* (Hentz), jumping spider. Fig. 3.—Most abundant salticid; matures and reproduces in summer, among herbs. Hot August apparently helpful. Most seen in 1936 and 1937.
- Zygoballus bettini* Peckham, jumping spider. Fig. 3.—In herbs; reproduces in serotinal and autumnal seasons. Moderate temperature and humidity in these seasons best.
- Cantharis* sp., and *Malthodes spado* Lec., soldier beetles. Fig. 3.—Adults seen only in late vernal or early estival seasons, *Cantharis* appearing later and staying longer than *Malthodes*. Possibly spend summer in trees. Larvae in ground in winter. Numbers alike in 1937 and 1938, but beetles seen earlier in 1938 than in 1937.

- Idiostethus tubulatus* Say and *I. subcalvus* Lec., weevils. Figs. 3 and 4.—Adults hibernate in soil and move to waterleaf in vernal season, when they are most abundant. Probably reproduce in estival season. Active earlier in 1938 than 1937, though the effect of weather on numbers is not known.
- Anyphaena pectorosa* L. Koch, spider. Fig. 4.—Among herbs and shrubs in summer. Reproduces in estival season; young spiders hibernate. Numerous in 1934, and more so in 1937 and 1938. Effect of weather not clear.
- Sapromyza crevecouri* Coq., fly. Fig. 4.—In herbs and shrubs in estival and serotinal seasons. Greatest numbers in 1937, less in 1938; very few in 1934 or 1935. 1936 data missing. Cause of differences not known.
- Leptothorax curvispinosus* Mayr, ant. Fig. 4.—Among herbs and shrubs in summer. Colonial on ground; thus soil records are of little value. Summer herb and shrub counts considered better; by these, the 1937 and 1938 populations were equal. Effect of weather not known.
- Phalacrus politus* Melsh, smut beetle. Fig. 4.—Described by Weese (1924) and Blake (1926). Few seen except in winter of 1935-1936. Effect of weather not clear.
- Hahnia cinerea* Emerton, spider. Fig. 4.—A soil dweller, seen least in the summer. Reproduces probably in the estival season. Effect of weather not known.
- Lathrobium* sp., rove-beetle. Fig. 4.—A soil resident, most abundant in the vernal season. More abundant in 1937 than in 1936 or 1938. Large winter population possibly due to warm weather making activity possible.
- Tracheoniscus rathkei* Brandt, sow-bug. Fig. 4.—Immature specimens on ground and in logs; no adults seen. More abundant in 1937 than in 1938; cause for this not known.

Discussion

From the descriptions given above it is clear that the population of an elm-maple forest is not static, but changes both from one season to another and from one year to the next. These fluctuations have been considered in relation to weather conditions and it has been seen that, while climate and the details of climate, namely weather, probably influence many animals, they apparently are not the sole direct controlling factors in regulating the abundance of invertebrates. Rice (1946) has emphasized the size of the overwintering group which emerges in spring and stressed the effect of birds in reducing hibernating populations.

The abundance of a species may be affected at any time of the year or at any point of the animal's life history. However, the susceptibility of an animal to adverse conditions is not always the same, but may differ at different stages of the life history. Requirements for optimum or maximum development of populations also differ similarly. Animals have physiological as well as morphological life histories, and conditions which are optimum at one state may be less so, or even detrimental, at another stage of the physiological life cycle.

Obviously, any factor which affects the number of eggs laid will affect the abundance of the species. Temperature may affect copulation and fertility (Uvarov, 1933); humidity may affect the rate of reproduction. Similarly, after the eggs are laid various factors may affect the per cent that hatch. Weather conditions are important for eggs, but other factors become

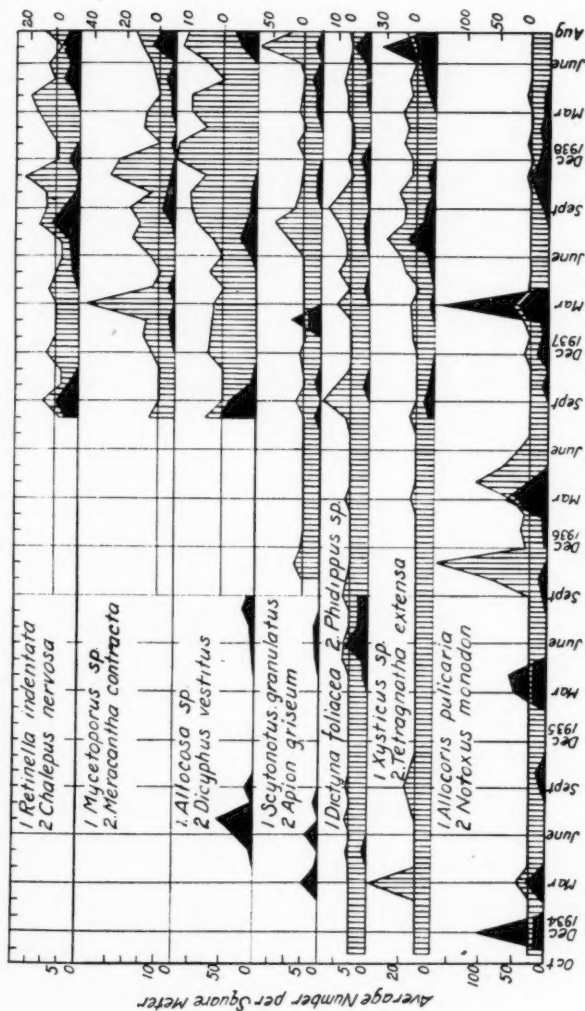


Fig. 2. Monthly averages of numbers per square meter of various invertebrates, plotted one above another.
1. Striped area. 2. Black area.

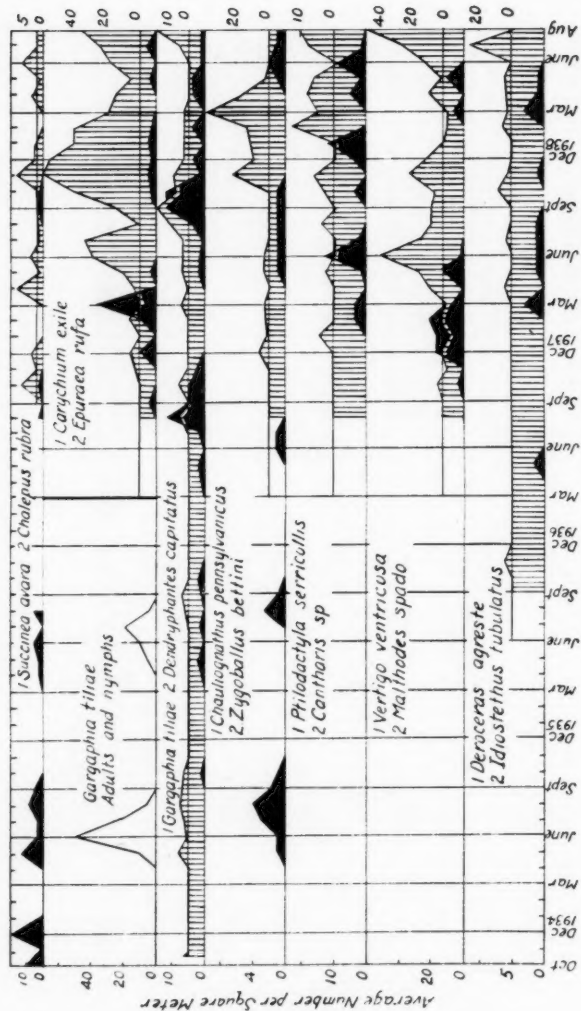


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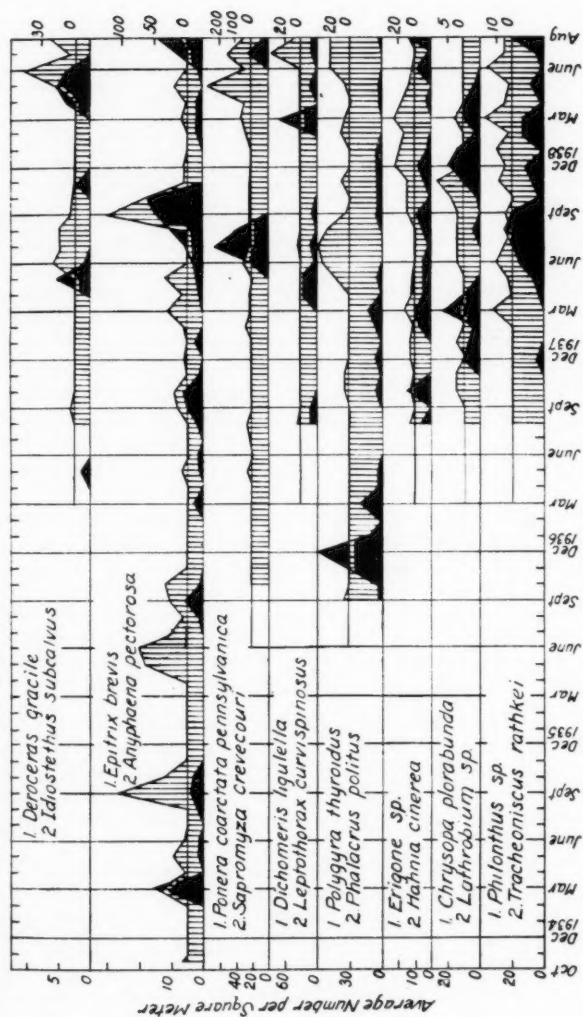


Fig. 4. Monthly averages of numbers per square meter of various invertebrates, plotted one above another. 1. Striped area. 2. Black area.

of importance to the young animal. The very young invertebrate is often more susceptible to adverse conditions than later stages, hence the per cent of animals which reach maturity is very low.

Weather conditions have already been discussed. Temperature, humidity, and precipitation have been considered, and it appears from the foregoing that these are of great importance. Light and wind may also be effective. Seasonal or monthly means of physical conditions may be important; or, as Shelford (1932) has shown for *Blissus leucopterus*, extreme conditions, e. g. of precipitation, in one day or night may modify the entire year's population. Extremes of temperature may kill many animals (Rice, 1946).

The enemies of a species are effective in helping to regulate its abundance (Rice, 1946). Enemies are primarily of two types, predators and parasites. Both of these are in turn influenced by climatic conditions, so that weather is a secondary controlling factor. Any condition which tends to reduce the number of predators or parasites of an animal tends to favor abundance of that animal. Weese (1924) and others have shown that the optimum conditions for the host species are not necessarily optimum for the parasite; the same is probably true for predators.

Food is another factor which influences the abundance of an animal. This has been seen in some phytophagous forms. The season of activity, and probably also the abundance, of *Epitrix brevis*, *Cantharis* sp., *Malthodes spado*, *Idiostethus tubulatus*, and *I. subcalvus* appear to depend more directly upon the presence of food plants than upon weather conditions. Blake (1931) observed that the time for leaving hibernation in the spring was in many cases dependent upon plants rather than weather conditions. It is difficult to distinguish the effects of food and weather in the field, for weather conditions influence the growth of plants very closely. No cases of variations depending upon the presence of animals as food have been observed, though they probably exist. Weather conditions here also are secondarily effective by helping to control the abundance of animals used as food.

The viability of an animal may vary in different stages. This is believed to be the case for *Agelena naevia*, which in the second instar has a much greater mortality than in the first or third instar. Also, the viability of an animal may vary from one year to another, as Shelford (1932) observed in the chinch-bug. This may have been the cause for some of the fluctuations observed in 1933-1938.

Some of the differences in the abundance and activity of animals have been indicated in the descriptions of the different species. As Smith-Davidson (1932) stated, the climax association appears to be formed of a great number of species, most of which are present usually in small numbers but which may with favorable conditions rise sharply in abundance. Smith-Davidson also stated that the season of activity of an animal may vary when weather conditions change; a few such changes have been noted. The spring of 1937 was colder than usual and in that year the beginning of activity of several animals was delayed. In 1938, on the other hand, the spring was very warm and moist, and the majority of the animals were active earlier than

usual (see Tables 1 and 2). An early appearance in 1938 has been seen in the cases of *Cantharis* sp., *Malthodes spado*, *Idiostethus* spp., and others, which were seen several weeks earlier in 1938 than in 1937.

The winter of 1935-1936 was very much colder than any of the other winters studied, with a mean seasonal temperature of 21° F. and a minimum of -21° F. The mean humidity was also lower than in any of the other winters. Such extremes seldom occur in the locality studied, and it is interesting to note the effect of the severe winter upon the animals. There are nineteen species whose abundance before and after this winter are known. Of these, four showed no change in numbers and therefore were presumably unaffected by the winter. Two species rose in abundance in 1936, and thirteen dropped in numbers. All these fluctuations cannot be attributed to the effect of the cold winter alone, for the summers of 1935 and 1936 were widely different, and thus probably affected the animals differently. Since the summers of 1933 and 1936 were very much alike, it is possible that the differences on populations observed in these two years were due to differences in the preceding winters. There are nineteen species whose abundance in both years is known. Of these, *Allocoris pulicaria*, *Epitrix brevis*, *Diabrotica vittata*, *Anyphaena pectorosa*, and *Zygoballus bettini* were equally abundant in 1933 and 1936. Seven species—*Dicyphus gracilentus*, *Phalacrus politus*, *Apion griseum*, *Dictyna foliacea*, *Pisaurina mira*, *Phidippus* spp., and *Dendryphantus capitatus*—were more abundant in 1936 than in 1933, and thus possibly were favored by the cold winter of 1935-1936. Seven species—*Lygus oblineatus*, *Gargaphia tiliae*, *Corythucha aesculi*, *Notoxus monodon*, *Chalepus rubra*, *Epitrix fuscula*, and *Xysticus* spp.—were more abundant in 1933 than in 1936. These data indicate that a severe winter may influence a population in either direction. The effect, however, is different for each species, and it is accurate to state that in a severe winter the populations of some species are reduced while those of other species are favored. Severe winters, like other weather conditions, do not appear to affect the community as a unit, but rather to influence it by affecting each species separately.

Tables 1 and 2 show hibernation dates for various species, determined by using the last date at which the animal appeared on herbs each fall and the first date at which the animal reappeared on herbs in the spring. The animals are arranged in approximate sequence, those entering the soil first in the fall being placed before those entering late, and the animals leaving the ground early in the spring being listed before those leaving the soil late. Comparison of the two tables shows that the animals are in approximately reverse order in the two tables; i. e., animals which begin hibernation early in the fall leave hibernation late in the spring, while those which remain active longer in the fall venture out earlier in the spring. Rutherford (1929) and others have made this observation before.

The time of hibernation in the fall may depend upon the mean temperature, the rate of drop of temperature, the minimum temperature, or a combination of these. Killing frosts may be important; yet some animals begin hibernation before such a frost occurs, while others remain active for a few

weeks after the time of the first killing frost. Possibly humidity is also effective, but its influence is little known.

The time of emergence of a species in the spring is probably affected by much the same conditions as the time of beginning of hibernation in the fall. Mean air temperature, rate of rise of temperature, the minimum temperature, or a combination of these may be influential, and similarly, soil temperature conditions are probably important for spring emergence. Relative humidity and precipitation can be of importance, as in the fall.

TABLE 1.—Dates of Last Appearance of Animals in Herbs Each Fall.

Animal	1933	1934	1935	1936	1937
<i>Glyphonyx testaceus</i>	Sep. 5	Sep. 6
<i>Heteroneura</i> sp.	Sep. 5	Sep. 13
<i>Sapromyzosoma incerta</i>	Sep. 12	Sep. 6
<i>Sciapus</i> sp.	Sep. 12	Sep. 13
<i>Hyaliodes vitripennis</i>	Sep. 19	Sep. 19	Sep. 19
<i>Lasius niger americanus</i>	Oct. 4	Sep. 6
<i>Succinea avara</i>	Sep. 12	Oct. 3
<i>Camponotus caryae</i>	Oct. 4	Sep. 19
<i>Myrmica punctiventris</i>	Sep. 19	Oct. 11
<i>Zygoballus bellini</i>	Oct. 2	Sep. 24	Oct. 3
<i>Sapromyza crevecouri</i>	Oct. 10	Sep. 19
<i>Polygyra thyroidea</i>	Sep. 24	Oct. 11
<i>Phytonomus nigrirostris</i>	Sep. 26	Oct. 12
<i>Chloropisca glabra</i>	Oct. 1	Oct. 11
<i>Notoxus bicolor</i>	Oct. 3	Oct. 4	Oct. 11
<i>Myrmica scabrinodis</i>	Oct. 24	Sep. 19
<i>Dikraneura abnormis</i>	Sep. 19	Oct. 25
<i>Corythucha aesculi</i>	Oct. 12	Oct. 10	Oct. 15	Sep. 19
<i>Thiodina puerpera</i>	Oct. 4	Oct. 11
<i>Leptothorax curvispinosus</i>	Oct. 4	Oct. 11
<i>Chalepus nervosa</i>	Oct. 12	Oct. 3
<i>Dicyphus gracilentus</i>	Oct. 3	Oct. 4	Oct. 25
<i>Parasphingophora multiseriata</i>	Oct. 12	Oct. 11
<i>Brachypterus urticae</i>	Oct. 3	Oct. 24	Oct. 11
<i>Scymus fraternalis</i>	Oct. 4	Nov. 8
<i>Cicadellidae</i> nymph	Oct. 12	Nov. 1
<i>Vertigo ventricosa</i>	Oct. 12	Nov. 1
<i>Phyllotreta sinuata</i>	Oct. 12	Nov. 1
<i>Jalysus spinosus</i>	Oct. 23	Oct. 17	Oct. 25
<i>Blissus leucopterus</i>	Oct. 23	Oct. 22	Oct. 12	Nov. 1
<i>Dendryphantes capitatus</i>	Oct. 17	Oct. 22	Oct. 24	Nov. 1
<i>Diabrotica vittata</i>	Oct. 23	Nov. 7	Oct. 1	Oct. 12	Nov. 8
<i>Empoasca</i> sp.	Oct. 3	Nov. 15
<i>Epitrix fuscula</i>	Oct. 23	Sep. 19	Oct. 22	Nov. 18	Nov. 1
<i>Acanthocephala terminalis</i>	Nov. 10	Oct. 3
<i>Apion griseum</i>	Oct. 12	Nov. 8
<i>Balclutha punctatus</i>	Oct. 12	Nov. 8
<i>Anyphaena pectorosa</i>	Oct. 22	Oct. 22	Nov. 18	Oct. 19
<i>Myodocha serripes</i>	Oct. 23	Nov. 1
<i>Notoxus monodon</i>	Oct. 17	Oct. 8	Nov. 29	Nov. 1
<i>Dictyna foliacea</i>	Oct. 22	Nov. 4	Nov. 1
<i>Phalacrus politus</i>	Oct. 27	Nov. 19	Oct. 24	Nov. 1
<i>Epitrix brevis</i>	Oct. 23	Nov. 7	Oct. 1	Nov. 13	Nov. 30
<i>Xysticus</i> sp.	Oct. 22	Nov. 18	Nov. 1

TABLE 1.—Date of Last Appearance of Animals in Herbs Each Fall—(Continued)

Animal	1933	1934	1935	1936	1937
<i>Piesma cinerea</i>	-----	-----	Nov. 12	-----	Oct. 25
<i>Misumenops</i> sp.	-----	Nov. 14	-----	-----	Oct. 25
<i>Gargaphia tiliae</i>	Oct. 12	Oct. 22	Dec. 20	Oct. 12	Nov. 22
<i>Erythroneura</i> sp.	-----	-----	-----	Nov. 13	Nov. 1
<i>Diabrotica 12-punctata</i>	Oct. 23	Nov. 28	-----	-----	Nov. 8
<i>Phlepsius irroratus</i>	-----	Nov. 7	-----	Nov. 18	Nov. 8
<i>Nabis</i> sp.	Oct. 23	Nov. 28	-----	Nov. 18	Nov. 8
<i>Drasophila quinaria</i>	-----	Nov. 28	Oct. 29	-----	-----
<i>Pisaurina mira</i>	-----	Nov. 28	-----	Nov. 13	Nov. 8
<i>Tetragnatha extensa</i>	-----	-----	-----	Nov. 18	Nov. 15
<i>Ormenis</i> sp.	-----	-----	Nov. 26	Nov. 21	Nov. 8
<i>Tetragnatha laboriosa</i>	-----	Oct. 28	Nov. 26	Nov. 21	Nov. 1
<i>Lygus oblineatus</i>	Nov. 18	Nov. 28	-----	Nov. 21	Nov. 22
<i>Chrysopa plorabunda</i>	-----	-----	-----	Nov. 21	Nov. 22
Number of species	12	29	17	46	54
Average date	Oct. 25	Oct. 22	Oct. 25	Oct. 19	Oct. 22

TABLE 2.—Dates of First Appearance of Animals in Herbs Each Spring.

Animal	1934	1935	1936	1937	1938
<i>Phyllotreta sinuata</i>	-----	-----	-----	Mar. 7	Feb. 6
<i>Tmorus angulatus</i>	-----	-----	-----	Mar. 14	Feb. 6
<i>Lygus oblineatus</i>	Mar. 15	Mar. 20	-----	Mar. 7	Feb. 6
<i>Erigone</i> sp.	-----	-----	-----	Mar. 7	Apr. 10
<i>Tetragnatha extensa</i>	-----	-----	-----	Mar. 31	Apr. 3
<i>Notoxus monodon</i>	Apr. 5	Apr. 10	Apr. 1	Apr. 4	-----
<i>Nabis</i> sp.	Apr. 5	-----	-----	May 2	Mar. 13
<i>Xysticus</i> sp.	Apr. 10	-----	Apr. 8	Apr. 18	Apr. 17
<i>Gargaphia tiliae</i>	May 8	May 9	-----	May 2	Feb. 13
<i>Empoasca</i> sp.	-----	-----	-----	May 2	Apr. 13
<i>Erythroneura</i> sp.	-----	-----	-----	May 2	Apr. 3
<i>Anyphaena pectorosa</i>	May 15	-----	May 15	Apr. 11	Mar. 27
<i>Blissus leucoplerus</i>	Apr. 5	Apr. 24	-----	May 2	Apr. 17
<i>Balclutha punctatus</i>	-----	-----	-----	May 2	Apr. 10
<i>Leptothorax curvispinosus</i>	-----	-----	-----	Apr. 25	Apr. 17
<i>Epitrix fuscula</i>	Apr. 17	May 9	-----	May 2	Mar. 27
<i>Corythucha aesculi</i>	Apr. 17	Apr. 24	Apr. 1	Apr. 25	Apr. 17
<i>Dendryphantes capitatus</i>	-----	Apr. 24	Apr. 30	May 2	Apr. 3
<i>Alloccoris pulicaria</i>	-----	Apr. 24	-----	May 2	Apr. 17
<i>Diabrotica vittata</i>	Apr. 24	Apr. 24	-----	May 2	Apr. 17
<i>Dictyna foliacea</i>	May 1	May 9	Apr. 16	Apr. 4	May 1
<i>Phalacrus politus</i>	May 8	Apr. 17	Apr. 30	May 2	Apr. 10
<i>Epitrix brevis</i>	May 8	May 9	May 8	Apr. 25	Mar. 20
<i>Ormenis</i> sp.	June 7	May 9	-----	Apr. 18	Mar. 13
<i>Tetragnatha laboriosa</i>	May 1	Apr. 24	Apr. 30	May 11	Apr. 10
<i>Jalysus spinosus</i>	Apr. 17	-----	-----	May 2	May 1
<i>Scymnus fraternus</i>	May 1	Apr. 24	Apr. 30	May 2	Apr. 24
<i>Idiostethus subcalvus</i>	-----	-----	May 8	May 2	Apr. 17
<i>Idiostethus tubulatus</i>	-----	-----	May 8	May 2	Apr. 17
<i>Balclutha impicta osborni</i>	-----	-----	-----	June 14	Apr. 17
<i>Apion griseum</i>	Apr. 17	May 31	-----	May 2	Apr. 17

TABLE 2.—Dates of First Appearance of Animals in Herbs Each Spring—(Continued)

Animal	1934	1935	1936	1937	1938
<i>Piesma cinerea</i>	May 2	May 1
<i>Camponotus caryae</i>	May 2	May 1
<i>Chalepus nervosa</i>	May 11	Apr. 24
<i>Chloropisca glabra</i>	Apr. 17	May 21	May 8
<i>Dolomedes</i> sp.	May 1	May 31	Apr. 18
<i>Dicyphus gracilentus</i>	May 8	May 9	May 18	Apr. 24
<i>Misumenops</i> sp.	May 15	May 9	May 11	Apr. 24
<i>Pisaurina mira</i>	May 1	May 15	June 14	Apr. 3
<i>Lasius niger americanus</i>	May 18	May 1
<i>Cicadellidae</i> nymph	May 18	May 8
<i>Vertigo ventricosa</i>	May 18	May 8
<i>Phidippus</i> sp.	May 22	Apr. 24	May 29
<i>Sciapus</i> sp.	May 2	May 29
<i>Malthodes spado</i>	May 25	May 8
<i>Tettigoniidae</i> nymph	May 11	May 22
<i>Pentatomidae</i> nymph	May 1	May 24	May 30
<i>Notoxus bicolor</i>	May 9	May 30
<i>Condylostylus</i> sp.	June 9	May 1
<i>Phytonomus nigrirostris</i>	June 13	May 31	Apr. 11
<i>Anthomyiella pratincta</i>	May 22	May 11	June 5
<i>Pentatomidae</i> nymph	June 9	May 15
<i>Cantharis</i> sp.	May 30	May 22
<i>Succinea avara</i>	May 25	May 29
<i>Glyphonyx testaceus</i>	May 18	June 5
<i>Sapromyzosoma incerta</i>	May 8	May 24	June 14	June 5
<i>Sapromyza crevecouri</i>	Apr. 17	June 14	May 29
<i>Formica fusca subsericea</i>	June 14	May 22
<i>Heteroneura</i> sp.	June 9	May 29
<i>Myrmica punctiventris</i>	June 14	May 29
<i>Nabidae</i> nymph	June 14	May 29
<i>Phlepsius irroratus</i>	June 17	May 24	June 7	June 28	June 5
Number of species	30	26	13	61	57
Average date	May 1	May 5	Apr. 29	May 7	Apr. 22

The average date of hibernation each year has been calculated. Collections during all the years of study have been made once a week; therefore an error of one week in either direction is possible, and the average hibernation dates probably have no value unless they differ by at least fourteen days. Therefore, by the present system of collecting, no differences of hibernation can be observed unless they are great, and minor changes from one year to another go unseen.

Another factor making the average dates unreliable is the great difference in the number of species observed. Very few were noted in 1933 and 1935, and the averages given for the falls of these years may be far from correct. Also, it is possible that all the species do not hasten emergence under the same conditions; in that case, average dates are useless.

The greatest differences in average dates of hibernation in the fall is six days and therefore the writer feels that there is no basis for assuming

that the beginning of hibernation each year has been different. Individual species, however, varied, some for a period as great as a month or more.

The greatest variation in spring emergence was between 1937 and 1938, with a difference of fifteen days. In 1937 emergence was later than usual, and in 1938 was earlier than usual. This difference is correlated with the difference in weather conditions during the late winter and spring of the two years. February of 1937 had normal temperature and humidity, while in 1938 this month was much warmer and more humid than usual. Table 2 lists several species which emerged during February of 1938. In 1937 March was much colder than usual and had a smaller range of temperature than in any other year. March of 1938, on the other hand, had the highest temperature and the greatest range of temperature of all the years studied. The soil temperature in March of 1937 was very low, and had by far the smallest range of all five years. March, 1938, had a very high soil temperature, with an average range. The humidity in March, 1937, was normal, but precipitation was low, while in 1938 March had a higher humidity and precipitation. The low soil and air temperature of March, 1937, probably acted to keep animals in the ground at that time, while the warm, moist conditions in 1938 probably hastened emergence.

April of 1937 was cooler than usual, but in 1938 was much warmer than usual. Soil temperature, rising more slowly than the air temperature, was very low in 1937, but unusually high in April of 1938. Possibly this difference was important in causing the differences in emergence that month. The moisture conditions in April of the two years were the reverse of those in March, for in April of 1937 humidity and precipitation were greater than usual, while in 1938 this month had normal moisture conditions.

In 1935 hibernation ended almost as late as in 1937, being on the average thirteen days later than in 1938. In 1935 February was warmer than usual, though soil temperatures were slightly below average. The humidity was very low, and precipitation was also less than usual. March was warmer than usual, in both the air and soil, but humidity was almost as low as in 1937. Precipitation was normal. Possibly the low humidity in February and March was a retarding factor. The air in April was cool, as was the soil. Humidity and precipitation were approximately normal. The cause for the delay in 1935 is not so apparent as in 1937, as is true also for the evidence of such a delay. Probably a combination of slightly unfavorable conditions was effective in 1935, whereas low temperature was evidently the most important factor in 1937.

Thus rising soil and air temperatures, probably combined with moisture conditions, seem to hasten emergence, while low, slowly rising soil and air temperatures, and probably low humidity, retard emergence. Rice (1946) stresses temperature and light.

It appears difficult to form definite conclusions as to the time of hibernation of invertebrates from the existing material. The five years' work presented here is of value partially in showing that the collecting method employed is inadequate for purposes of analyzing hibernation. It is a special problem requiring special methods and frequent collections during the migra-

tion period. Daily collections are desirable, and certainly one collection each two days is needed. With data for every other day, variations of four days in different years are significant. Information on animals present in small numbers needs to be more complete in order to follow the beginnings and increases of individuals and moving populations. Frequent collections should be made from the first of September through November, and from the first of March until the first of June, though few samples need be taken during the hiemal season. In most years the first half of March is unimportant in relation to migration and may be neglected, but in some years early collections are necessary. In 1938, for instance, several species moved to the herbs even in the middle of February and were seen in that layer steadily after that time. Weather conditions and occasional checks on the animals in the field should determine the time for regular collections, which may vary from year to year.

Possibly, with more information concerning hibernation, it will be found that the periods of migration peaks are of more value than the dates of first and last appearances in the upper layers. Such peaks cannot be determined accurately for many species when collections are made only once a week. The dates of the first and last appearance in the herbs are of doubtful value because animals may move up to the herbs for a short time on warm spring days, and then return to the soil for several succeeding days; and, conversely, on cool autumn days the animals may go to the soil, to return to the upper layers later. This is probably the case with *Polygyra thyrionus*, which early forms an epiphragm which probably is removed before true hibernation begins. Proper evaluation of such shifts is difficult.

Very careful observation of weather conditions is also necessary in the study of hibernation. Not only weekly or daily conditions need be known, but also the conditions when the collections were made. Preferably all the collections will be made at the same time each day, so that differences in diurnal cycles will not influence the record of seasonal changes.

For the study of annual changes in animal populations and the relation of these changes to weather conditions, five years form a period too short to be of value in any way except to indicate the possible relations between climate and abundance, without in the least forming positive proof of these relations. The writer has presented many hypotheses concerning the effect of temperature and moisture upon various species; however, she states these relations with realization of their weaknesses, and recognizes that later work may disprove all of them. Some of the virtues of continued observations are already apparent. Kanatzar (1936), considering the fluctuations of abundance of *Anyphaena pectorosa* in 1933-1936, concluded that cold weather reduced the numbers of this spider, but the relations between temperature and abundance did not continue in 1936-1938. Possibly Kanatzar's views are correct, but this cannot be determined from the present data, and the question can be settled only with more work. Further study will also either corroborate or disprove other explanations, and may clarify the changes in numbers of the animals whose relations to climate cannot be stated even tentatively.

The ideal community study over a long period of time would be conducted by a single investigator or the same group of investigators. Personal differences in methods of collecting, sorting, and evaluating animals would thus be eliminated.

Lastly, it seems desirable to keep records of as many species as possible. All of these species are not abundant, and may never be, yet the present report shows that the population of a forest varies, and that a species may rise to unexpected numbers in one season or year and return to the usual low numbers in the next year. If the records of such species during the years of less abundance can be added to those for the years of great abundance, an interpretation of the changes may be possible.

Conclusions

1. At William Trelease Woods during 1933-1938 the abundance of various invertebrates has varied sharply. Not all the invertebrate species in one locality respond in the same way to weather conditions, but one set of conditions affects different species differently. Following the severe winter of 1935-1936 some species increased and some decreased in abundance.

2. During hot, dry seasons the majority of invertebrates in an elm-maple forest are less abundant than in moderately warm, humid seasons. In the warm, damp spring of 1938 most invertebrates emerged from hibernation earlier than in the cold spring of 1937.

3. The time at which animals begin or end hibernation can be determined only by frequent collections during the period of migration into or out of hibernation. The causes of many common phenomena in invertebrate populations will be better understood if a community study is continued over a period much longer than five years.

4. Weather conditions cannot explain all the variations in invertebrate populations; other factors must exert at least a slight effect.

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Comparative Morphology and Taxonomy of the Capniidae (Plecoptera)¹

John F. Hanson

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Introduction

Studies of external anatomy of various widely differing species of insects have been published; but detailed comparative studies, particularly within the lower taxonomic categories (genera and species), are few. Not until such studies are made can one expect to understand the phylogenetic and taxonomic relationships of the insects concerned. It is the author's hope that this paper partially fulfills a need for such work in one small niche of taxonomic entomology.

Originally the author intended to confine this study to a treatment of thoracic morphology. However, it early becomes apparent that many very interesting variations in other body regions occurred and that these might have morphological and taxonomic implications of considerable importance. There-

¹ The material represented in this article was originally submitted at Massachusetts State College as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

fore the work was expanded to include a morphological consideration of all skeletal parts of all obtainable species in the family Capniidae. The taxonomic distinctions and interrelationships disclosed as a result of this morphological study are discussed in the second part of this paper.

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Part I. External Anatomy of *Capnia nigra* (Pictet)

Capnia nigra (Pictet) is the type species of the typical genus of the Capniidae. Consequently all conclusions concerning family and generic characters are ultimately based upon it. It is appropriate, therefore, that a study of the comparative morphology of the family Capniidae be introduced by a detailed discussion of the anatomy of this species.

Figures of nearly all external anatomical features of *Capnia nigra* are included to supplement the discussion. The treatment of the comparative morphology of other genera of Capniidae is supplemented by figures wherever characters of generic significance occur.

The study of this species was made possible through the loan of material by Professor N. Banks of the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. The identity of the specimens studied is unquestionably in agreement with *Capnia nigra* as used by European workers. Morton especially (1929) has figured the species in detail. As far as I can determine no author has studied the genitalia of the type specimens. It is even doubtful that the types still exist.

General Appearance

Capnia nigra, like most other species of the genus, is a relatively small, slender, darkly colored stonefly. It varies from 5 to 6 mm. in length in the male sex and from 6 to 8 mm. in the female. The female is fully winged but the male is extremely brachypterous, having practically veinless wings which are reduced to one millimeter or less in length. In both sexes the wings and most of the sclerotized body parts are covered with tiny light-colored setae.

Head

Figs. 1-3, 5-10

The head of *Capnia nigra* is prognathous and somewhat flattened. Its length is about equal to its width which is greatest at the compound eyes. The

mandibles, antennae, and eyes are located laterally on the head; the ocelli are located dorsally.

SUTURES OF THE CRANIUM OR HEAD CAPSULE

The principal sutures of the cranium of *Capnia nigra* are the *postfrontal*, *postoccipital*, *subgena*¹ *epistomal*, *ocular*, and *antennal* sutures.

The EPICRANIAL SUTURE is not completely developed, since *frontal* sutures rarely if ever occur in Plecoptera (Crampton, 1932); and in *Capnia nigra* with which we are here concerned the *coronal* suture also is either entirely absent or only very weakly indicated.

POSTFRONTAL SUTURES (pfsu), which may be confused easily with frontal sutures, are present and are well demarked. From a mesal point on the vertex, where they meet at a very obtuse angle, each postfrontal suture extends along a straight line to the posterior margin of the lateral ocellus and then curves sharply around the outer edge of the ocellus. Within a very short distance anterior to the ocellus it terminates at the posterior end of the tentorial callosity.

THE POSTOCCIPITAL SUTURE (pocs) closely parallels the dorsal and lateral margins of the foramen magnum. Near its anterolateral extremities it is weakly marked. There is no *occipital* suture.

THE SUBGENAL SUTURES each consist of two portions, the *pleurostomal* and *hypostomal* sutures. Each of the paired *pleurostomal* sutures (pls) seem to be identical with the linear exterior edge of the anterior tentorial pits formed by the fan-shaped anterior tentorial arms. Each *hypostomal* suture (hms) follows closely the cranial margin between the lower mandibular articulatory point and the posterior tentorial pit.

THE EPISTOMAL SUTURE (es) is a very distinct suture connecting the two anterior tentorial pits across the front part of the cranium. This suture is produced by a deep inflexion resulting internally in a strong *epistomal* ridge (esr) which forms a brace between the upper articulatory points of the mandibles.

OCULAR SUTURES (os), surrounding the compound eyes at their bases, are present.

AN ANTENNAL SUTURE (as) entirely surrounds each *antennal* socket close to its edge.

AREAS OF THE HEAD CAPSULE

The principal areas of the cranium are the *clypeus*, *frons*, *parietals*, *postocciput*, *genae*, *subgenae*, and *postgenae*. Not all of these are demarked by sutures.

THE CLYPEUS (cl) is a small, transverse sclerite bounded anteriorly by a membranous region between it and the labrum, and posteriorly by the epistomal suture.

The FRONS (fr) is a large area bounded anteriorly and posteriorly by the epistomal and postfrontal sutures, respectively. Laterally it is bounded by the antennal sockets and the tentorial callosities.

Immediately anterior to the median ocellus, which is situated near the middle of the frons, a transverse suture extends for a very short distance to either side of the ocellus. In one genus of Capniidae this suture completely divides the frons into two parts. It has been suggested to me by Dr. Crampton that this suture, which in practically all stoneflies is a very short and inconspicuous suture in front of the median ocellus, may be the actual frontal suture. In such a case the true frons would be confined to the region between the clypeus and the median ocellus; the frontal region posterior to the median ocellus would probably have to be considered to be a secondary postfrons. However, since this view is by no means proven, it seems advisable to recognize the entire area from the postfrontal sutures to the clypeus as the frons in conformity with the interpretations of Crampton (1932) and Hoke (1924).

The TENTORIAL CALLOSITIES (tc) are two slightly convex areas of the dorsal cranial surface corresponding to the points on the intenal surface of the cranium where the dorsal tentorial arms abut against it. They usually lie within the frontal area. In *Capnia* they are relatively large oval areas whose long axes coincide with an imaginary line connecting either lateral ocellus with the nearest point of the antennal socket of the same side of the head.

All three OCELLI (oc) are borne on the frons. The *lateral ocelli* are situated close to the lateral angles of the postfrontal sutures. The distance between them is slightly less than three times the distance of either ocellus from the compound eye nearest to it. The *median ocellus* is slightly closer to the epistomal suture than to the median point of junction of the postfrontal sutures.

The PARIETALS (par), due to the absence of a delimiting coronal suture, merge into a large transverse area in the posterior part of the cranium. On each side of the head this plate extends to meet the gena at the constricted region between the antennal socket and the compound eye. It also extends laterally behind the compound eye to the postgenal region on the lower surface of the head. The dorsal area of the parietal sclerite is known as the *vertex*. The latter region usually bears a few longitudinal embossings.

The ANTENNAL SCLERITES (asc) consist of narrow but distinct bands surrounding the antennal sockets. Each has an anterodorsal and an antero-ventral *antennifer* (af) or expanded articulatory point.

The OCULAR SCLERITE (osc) is a narrow internal rim or shelf around the margin of the compound eye. It is easily visible through the outer cuticle of the eye in cleared specimens.

The COMPOUND EYES (eye) are situated laterally on the head. They are slightly oval or nearly round in outline and protrude conspicuously (nearly hemispherically) from the cranium. Each compound eye is composed of approximately 200 ommatidia.

The POSTOCIPUT (poc) forms the posterior rim of the cranium. It is

a narrow, roughly horseshoe-shaped or U-shaped sclerite whose ends terminate at the posterior tentorial pits. Ventrolaterally its posterior margin is produced on each side into a small *occipital condyle* (occ) with which the *cephalinger* (cep) of the corresponding lateral cervical sclerite articulates.

The SUBGENAE consist of two pairs of tiny, elongate sclerites. Each *pleurostoma* (pm) is a very tiny plate situated between the base of the mandible and the antennal socket. Each *hypostoma* (hm) is a narrow band or thickening bordering the foramen magnum between the lower mandibular articulatory point and the posterior tentorial pit.

The GENAE (ge) are a pair of undifferentiated ventral areas on either side of the head between the hypostoma and the eye.

The POSTGENAE (pge) are a pair of undifferentiated ventral areas below and behind the compound eyes on either side of the head.

TENTORIUM

The *tentorium* (Fig. 2) consists of a *corporotentorium* (ct) in the center of the head and three pairs of arms supporting it from different parts of the cranium. The *anterior* (ata) and *posterior* (pta) *tentorial arms* are formed by invaginations of the cranium. The *dorsal tentorial arms* (dta) are said to arise as outgrowths of the anterior tentorial arms.

The ANTERIOR TENTORIAL ARMS (ata) arise from the anterior tentorial pits which are curved sutures extending from the dorsal antennifer to the ventral antennifer. Thus, each anterior tentorial arm is a scoop-shaped, lamellar structure the outer end of which is continuous with the anterior section of the antennal sclerite. It tapers rapidly to its point of attachment with the corporotentorium.

The POSTERIOR TENTORIAL ARMS (pta) arise from the posterior tentorial pits which are oval openings at the anteroventral extremities of the postocciput. They are shorter, narrower, and stouter than the anterior tentorial arms.

The DORSAL TENTORIAL ARMS (dta) are longer and narrower than those described above. They appear to arise at the region of fusion of the anterior tentorial arms with the corporotentorium. They narrow slightly ectally toward their abruptly expanded peltate apices which abut against the internally concave *tentorial callosities* (tc).

The CORPOROTENTORIUM (ct) or "body" of the tentorium is the central, somewhat sagittally elongate portion to which all tentorial arms are entally attached.

HEAD APPENDAGES

The movable parts of the head are the following: *antennae*, *labrum*, *mandibles*, *maxillae*, *hypopharynx*, and *labium*.

The ANTENNAE are setaceous and are about equal in length to the length of

the head and thorax combined. They are composed of a series of segments varying between 25 and 30 in number. The basal segment or *scape* (s), which is short and thick, articulates basally with the antennal sclerite at two points (with the upper and lower antennifers) and distally with the *pedicel* (p) at two points in a plane at right angles to the plane of movement of the scape. The combination of these two articulations forms a universal joint allowing movement of the flagellum in all directions. The *pedicel* is shorter than and of only about half the diameter of the scape. The *flagellum* is nearly immovably articulated with the pedicel at its base. Constricted regions in the apparent first segment of the flagellum indicate that it is a fusion of the first two and sometimes three original segments. It is thus usually about twice as long as the segments immediately following it. The second flagellar segment is much smaller than the first. From this segment nearly to the end of the antenna the length of the segments increases. The size of a few of the apical ones is slightly smaller than that of the subapical segments.

The LABRUM (lr) or upper lip, though not a true appendage, is movable and functions as one of the mouthparts. It is a transverse, roughly quadrangular sclerite attached to a membranous region in front of the clypeus. It is slightly convex above and slightly produced along its distal margin. Its lateral *tormae* extends into the membranous region at its base but do not articulate with the clypeus.

The MANDIBLES (Figs. 9, 10) are well developed and asymmetrical. Curved opposable *molar* surfaces (mo) crossed by many fine ridges, apparently for grinding food, are located at their inner angles. The molar area of the left mandible is concave while the opposable mola of the right mandible is convex. The left mandible bears four *teeth*; one submarginal on the dorsal or concave surface near the mola, and three marginal apical ones. The right mandible bears three teeth; one submarginal on the ventral or concave surface near the mola, and two marginal apical ones.

The base of the mandible is triangular in shape. A strong *flexor tendon* is attached to the inner angle of the base. To the sharp lateroventral angle a weaker *retractor tendon* is attached. On the margin between these two tendonal attachments close to the retractor tendon is a conspicuous condyle which articulates with the pleurostomal margin on the lower surface of the cranium. The upper angle of the base bears a smaller condyle that articulates in a socket of the subgena contiguous with the lateral basal angle of the clypeus.

The MAXILLAE (Figs. 5, 6) are composed of several distinct parts; namely, *cardo*, *stipes*, *parastipes*, *lacinia*, *galea*, and *palpus*. The axis of the *cardo* is oriented at about right angles to the sagittal line while the remainder of the maxilla assumes a sagittal position closing the preoral cavity laterally.

The *cardo* is divided by a distinct suture into two nearly equally sized convex sclerites, the *basicardo* (bc) and the *disticardo* (dc). The dividing suture extends from the single proximal articulatory point of the *cardo* on the anterior margin of the posterior tentorial pit to a distal ventral articulatory point. Another distal articulatory point occurs on the dorsal edge of the disti-

cardo. The resulting dicondylic hinge thus permits of horizontal motion of the outer parts of the maxilla.

The *stipes* (si) which is the largest sclerite of the maxilla is situated mostly on the ventral surface, but also is reflected slightly onto the dorsal surface of the maxilla.

The *parastipes* (ps) is a narrow sclerite demarked from the mesal edge of the stipes. It is broadest at about the middle, is very narrow basally, and is pointed distally.

The *lacinia* (la) is the inner of two lobes borne apically by the stipes. It is a well sclerotized, roughly pyramidal or cone-shaped structure attached on its ventral surface to the stipes by a dicondylic hinge. Dorsally its base is connected with a well sclerotized but very small *retractoral plate* (rp). Numerous strong muscle fibers extend from this plate to the wall of the stipes near its proximal end. The lacinia is hinged in such a manner that contraction of these muscles obviously must move the lacinia inwardly. Doubtless this mechanism constitutes one of the chief means by which food is manipulated into the preoral and oral cavities. The mesal edge of the lacinia is a sharp ridge bearing a subapical fringe of long setae and a sharp bidentate apex that is well adapted to such a function as that described above.

The *galea* is the outer lobe borne distally by the stipes. It is divided into a small, poorly defined, poorly sclerotized *basigalea* (bg) and a large, well defined *distigalea* (dg) of about the same length as the lacinia. The distigalea is a bluntly pointed structure bearing two longitudinal membranous regions and numerous apparently sensory papillae.

The 5-segmented *maxillary palpus* (mxp) arises laterally in the membranous region near the base of the galea; there is no differentiated palpifer. Its basal segment is the shortest and its apical segment is the thinnest. In ascending order of size the sequence of segments is as follows: 1, 2, 3 and 5, and 4.

The *HYPOPHARYNX* (Fig. 7) of *Capnia* is a large, thick lobe filling the preoral cavity and apparently consisting only of the lingua. Superlinguae are not present. Its bulbous anterior end is unsclerotized and is slightly bilobed. Its distal surfaces bear innumerable minutely microscopic spinulae which offer a rough surface for manipulation of food.

The so-called *basal plates* or *bars* (bpl) are fused into a single process for most of their length. The entire structure consists of a long, thin, basal section which forks into two diverging, distal arms that lie on either side of the hypopharynx and extend nearly to its apex.

The *suspensoria* (sus) consists of five tiny plates; namely, an unpaired plate and two sets of paired lateral plates lying directly above the apices of the arms of the fused basal plates. Each of the lower pair of suspensoria articulates with an arm of the basal plates and with the unpaired plate above it. The unpaired plate extends across the front of the hypopharynx to articulate with both lower plates and also with the other or most dorsal pair of plates. The

latter articulate at their dorsal ends with the mandibles in the region of the attachment of the flexor tendon of each.

The small *mouth* (mh) opening lies in a groove in the hypopharynx between the upper pair of suspensorial plates. The unpaired suspensorial plate crossing the front of the hypopharynx supports the lower margin of the mouth. The mouth is opened or closed by the action of the mandibles. As the chewing surfaces of the mandibles are adducted the points of attachment of the suspensoria to the two mandibles move farther apart. This movement, which causes the spreading apart of the upper pair of suspensoria and a play of interaction between all the suspensorial plates, opens the mouth. By the reverse of the same mechanism, closure of the jaws closes the mouth.

The LABIUM (Fig. 8) closes the preoral cavity ventrally.

The *postlabium* or basal section is composed of a large submentum and a small mentum. The *submentum* (sm) is the largest demarked area of the labium. In shape it is transverse and trapezoidal. Its base merges with the membranous neck region. Its distal margin is completely demarked from the mentum. The *mentum* (mn) is a much smaller and more transverse sclerite than the submentum from which it is demarked by a straight line. Its distal margin is arcuately emarginate and a small mesal region is fused with the prelabium.

The *prelabium* is smaller and narrower than the postlabium. However, its length is greater than that of the postlabium. The *labiostipites* (lbi) is its largest portion. This protrudes basally into the mentum with which, as mentioned above, it is mesally fused. Distally it is constricted in the region of attachment of the palpi to almost one-third of its greatest width. Beyond the bases of the palpi it expands again to accommodate the bases of the glossae and paraglossae. The *glossae* (gl) are well demarked below from the labiostipites by a darkly sclerotized rim. Each glossa bears a small nipple apically. The *paraglossae* (pgl) are the same length as the glossae but are slightly broader than the latter. Basally they merge with the labiostipites. Basolaterally each is bounded by a darkly sclerotized rim. Both glossae and paraglossae bear sensory papillae at their apices. The *labial palpi* are 3-segmented and have no demarked palpiger at their bases. When extended they reach forward about the same distance as do the glossae and paraglossae. The second segment is always the longest, the third segment is very short and usually nearly hemispherical.

Cervix or Neck

Fig. 25

The cervix or membranous neck region (Fig. 25) between head and prothorax bears three sclerites, the *ventral cervical sclerite* and a pair of *lateral cervical sclerites*.

The VENTRAL CERVICAL SCLERITE (vc) lies free, immediately anterior to the prothoracic presternum. It is slightly smaller and more oval than the lateral cervicals.

The LATERAL CERVICAL SCLERITES (lc) are roughly hemispherical protrusions that are attached posteriorly to the prothoracic precoxal bridge and each of which sends a stout projection cephalad to articulate with an occipital condyle of the head.

Thorax

Figs. 17, 25, 31-33, 36, 37

THORACIC TERGA

Fig. 37

PRONOTUM.—The prothoracic tergum consists of a single large sclerite, the pronotum (pn), which is roughly square in shape. The lateral margins are deflected so as to encroach slightly on the pleural region. Near its anterior margin and running parallel to it is a suture delimiting the narrow transverse *precosta* (pc) (Snodgrass, 1935). Near the posterior border of the pronotum is a similar suture. In some stoneflies these two sutures are continuous with lateral submarginal grooves and collectively constitute the *marginal groove* (Claassen, 1931). A poorly defined mid-dorsal line connects the two above mentioned sutures. The *disc* or dorsal area of the pronotum bears a few irregular embossings on either side of the mid-line.

MESONOTUM.—The mesothoracic tergum is demarked into four main regions: *prescutum*, *scutum*, *scutellum*, and *postscutellum*; and other minor regions.

The **PRESCUTUM** (psc) is the anterior-most mesotegal sclerite. Its broad posterior margin protrudes arcuately into the larger scutum to its rear, and the narrower anterior end projects downward and under the posterior edge of the pronotum. It is divided along the mid-dorsal line by a distinct suture.

The **PREALAR BRIDGES** (pra) are distinct sclerites broadly joined to either side of the prescutum. Each bridge curves around the wing base and narrows to a blunt end abutting against, but not united with, the anepisternum in the pleural region (Fig. 36).

The **SCUTUM** (sct), the largest sclerite of the tergum, is roughly hexagonal in shape. The *anterior notal wing processes* (anp) consist of a pair of tiny projections at the anterior lateral angles of the scutum. The *posterior notal wing processes* (pnp) are larger and better demarked than the former, are triangular in shape, and are supported not only by the scutum but also along a line of union with the postscutellum.

The **SCUTELLUM** (scl) is a partially demarked region in the posterior part of the scutum. It is bounded laterally and posteriorly by a U-shaped suture; its anterior end is undemarked from the scutum. The scutellum of the male of *Capnia nigra* is not demarked from the scutum except in its posterior region where a section of the demarking suture persists. This condition may possibly be correlated with the lack of functional wings in the male sex of this species.

The **POSTSCUTELLUM** (pscl) is a rectangular and somewhat transverse sclerite united along its anterior border with the posterior notal processes, the

scutum, and the scutellum, and to the metathoracic presternum and prealar bridges along its posterior border. In the middle of this sclerite is a slightly raised lighter colored transverse area. On either side and to the rear of this are a pair of larger and more rounded light colored areas.

There is no *postalar bridge* in the mesothorax of *Capnia*.

METANOTUM.—The metathoracic tergum is smaller than that of the mesothorax but is otherwise very similar to it. It differs, however, in the following details. The *prealar bridge* (*pra*) is much smaller and less sclerotized than that of the mesothorax, and is not united with the prescutum as is the case in the mesothorax. A complete *postalar bridge* (*poa*) occurs in the metathorax and appears to be formed by an extension of the dorsal edge of the epimeron which unites with the lateral margin of the postscutellum.

THORACIC PLEURA

Fig. 36

PROPLEURON.—The prothoracic pleuron is composed of the primitive *eupleuron* and *eutrochantin* (Crampton, 1926). Plecoptera are the only pterygotan insects to retain the apterygotan condition in which eupleuron (*ana-pleurite*) and eutrochantin (*coxopleurite*) are distinct sclerites.

The **EUPLEURON**, the larger of these two regions, is divided into two main parts by the nearly vertical *pleural suture* (*pls*). The small region posterior to the pleural suture corresponds to the upper region of the definitive epimeron (Crampton, 1926). The larger region anterior to the suture corresponds to the upper region of the definitive episternum. Extending anteriorly and ventrally from the latter, and well demarked from it, is the *precoxal bridge* (*pr*) which in this genus and in all other Capniidae is well sclerotized and is united with the basisternum to form a complete precoxal bridge.

The **EUTROCHANTIN** (*etn*) (Crampton, 1926) is also divided into two regions by the pleural suture. It is thus composed of a very tiny posterior portion which corresponds to the lower region of the definitive epimeron and a larger anterior arm which corresponds to the lower region of the definitive episternum. The latter curves ventrally to articulate with the anterior proximal edge of the coxa.

A **POSTCOXAL BRIDGE** (*po*) is present but not quite complete in the pleural region, i.e. there is a small gap separating it from the epimeron.

MESOPLEURON.—The mesopleuracic pleura are more highly evolved than the prothoracic pleura.

A **PLEURAL SUTURE** (*pls*) extends obliquely cephalodorsad from the pleural coxal articulation or coxifer to the alifer of the wing, dividing the pleuron into two main regions, the *epimeron* and the *episternum*.

The **EPIMERON** (*epm*) is the upper, posterior, and smaller of the two main regions of the pleuron. It is bounded above by the articular corium of the wing,

and posteroventrally by the coxal articulatory corium. It is broadest posteriorly, and narrows to a pointed anterior apex at the base of the alifer.

The EPISTERNUM is subdivided by a poorly demarked, angular suture into two secondary regions known as *anepisternum* and *katepisternum*.

The ANEPISTERNUM (aes) projects upward to form three wing processes, the *anterior* (ab) and the *posterior basales* (pb) and the *alifer* (al). The *anterior basale* (ab) is shorter and broader than the other two pleural wing-base processes and is rounded apically. It is strengthened by a longitudinal ridge near its anterior margin. Its posterior margin is projected internally in a knife-blade-like ridge which lies close to the inner surface of the posterior basale. The two basales are connected by only a very thin membrane so that free movement of the anterior basale in response to the action of muscles attached to its internal ridge is allowed along a vertical sagittal plane. The *posterior basale* (pb) projects higher than the anterior basale and expands apically to form two points of articulation with the wing-base. Both basales merge at their bases with the anepisternum. In the male of *Capnia nigra* which is strongly brachypterous, the two basales are fused together. The *alifer* (al) is the smallest of the three pleural wing processes. It is heavily sclerotized and appears to be formed largely of the pleural ridge; but possibly its base is formed partly by a small narrow portion of the anepisternum and also by a portion of the epimeron.

The KATEPISTERNUM (kes) or lower region of the *episternum* is smaller than the anepisternum. It lies as a narrow strip between the anepisternum and the basisternum and then extends posteriorly and dorsally to meet the pleural suture along a broad margin.

The TROCHANTIN (tn) arises from the lower posterior region of the katepisternum, and its base lies deep within the latter.

There is no postcoxal bridge in this segment.

METAPLEURON.—The metathoracic pleuron is similar to that of the mesothorax described above. Only the following few minor differences occur. The pleuron as a whole is smaller than that of the mesothorax but the *epimeron* (epm) is larger having a greater dorsal development resulting in the formation of a complete postalar bridge not present in the mesothorax. The *katepisternum* (kes) is better demarked from the basisternum in this segment than it is in the mesothorax, and the *trochantin* (tn) does not encroach upon the katepisternum to the extent that it does in the mesothorax.

THORACIC STERNA

Fig. 25

PROSTERNUM.—The prothoracic *presternum* (prs) lies just anterior to the accurately emarginate margin of the basisternum. It is a small, nearly round sclerite.

The BASISTERNUM (bs) is the largest prosternal sclerite. To its broad

anterior region the precoxal bridges are fused; the postcoxal bridges are fused to its smaller posterior end and to the outer edges of the furcae.

The FURCASTERNUM (fs) is a small transverse sclerite situated at the posterior end of the basisternum and demarked from it by a distinct suture that extends from one furcal pit to the other (*sternacostal suture*).

The POSTFURCASTERNUM (pfs) is a larger sclerite than the above. In shape, it is transversely oval, exhibiting a tendency toward a division into two parts by membranization along the mid-ventral line. It is entirely isolated from other sclerotized regions by membrane.

The SPINASTERNUM (ss) appears to be more closely associated with the mesothorax than with the prothorax. However, since the spinasternum is usually considered to be the posterior-most sclerite of a thoracic segment (Crampton, 1926), I have provisionally adopted this view and am considering the anterior-most spinasternum of the thorax as a prothoracic structure. It is an extremely narrow, transverse, bow-shaped sclerite nearly as wide as the entire segment. It has an abrupt expansion at the middle and is fused at its apices to the anterior lateral angles of the mesothoracic basisternum.

MESOSTERNUM.—The presternum (prs) of the mesothorax is a small oval sclerite situated in the space enclosed by the prothoracic spinasternum and the mesothoracic basisternum.

The BASISTERNUM (bs) of the mesothorax is much larger than that of the prothorax. Therefore, the mesothoracic coxae are more widely separated from each other than are those of the prothorax. The basisternum is a transverse sclerite with an arcuately emarginate anterior margin and an arcuately protruding posterior region. It is bounded along an extensive lateral margin by the katapisternum of the pleuron. From the latter it is well demarked except posteriorly where for a short distance the demarking suture drops out. As mentioned previously, the anterior lateral angles of the mesobasisternum are fused to the prothoracic spinasternum.

The FURCASTERNUM (fs) is a small, slightly transverse sclerite which is strongly united with, but well differentiated from, the basisternum. The furcal pits of this segment are slightly farther apart than are those of the prosternum. A very distinct, semicircular, *submarginal suture* whose ends terminate near the anterior ends of the furcal pits gives a semicircular appearance to the furcasternum. This submarginal suture demarks a distinct posterior marginal band which is fused mesally with the elongate spinasternum and laterally is continuous with a pair of furcasternal arms. The *furcasternal arms* (fsa) are a pair of elongate processes extending from the furcal pits toward the coxae. Although they are not articulated with the coxae they appear to be adapted to offer them very strong support in the movement of the legs.

The SPINASTERNUM is a small, mesal, sagittally elongate, and well sclerotized plate which is united with the posterior region of the furcasternum and usually extends slightly under the metathoracic presternum at its posterior end.

The POSTFURCASTERNUM (pfs) is divided into two roughly circular plates lying on either side of the spinasternum.

METASTERNUM.—The *presternum* (prs) of the metathorax lies close to the strongly arcuate anterior margin of the basisternum and is triangular or rounded in shape. It is at least twice as large as the mesothoracic presternum.

The BASISTERNUM (bs) is smaller and more transverse than that of the mesothorax. Finger-like projections occur at its anterior lateral angles at the positions corresponding to the points on the mesothoracic basisternum where fusion with the apices of the spinasternum occurs. The basisternum is often completely differentiated from the katepisternum by the demarking suture.

The FURCASTERNUM (fs) is an extremely narrow, transverse sclerite strongly united with, but well differentiated from, the basisternum. It is not united with the first abdominal sternite. The *furcal pits* (fsp) are widely separated. The *furcasternal arms* (fsa) are smaller than those of the mesosternum.

There is no metathoracic spinasternum.

WINGS

Figs. 17, 36, 37

ARTICULATION WITH THE THORAX

FORE WING.—The axillary sclerites (Figs. 36, 37) figure prominently in this most complicated of hinges, the wing articulation of insects.

The FIRST AXILLARY SCLERITE of *Capnia nigra* is an elongate plate situated between the lateral edge of the scutum and the second axillary sclerite. Anteriorly the first axillary is produced into a long "neck" supported on the inner side by the anterior notal process and abutting on the outer surfaces against the base of the radial vein. Apically the "neck" articulates with the base of the subcostal vein. The first axillary sclerite is not visible in the lower wing membrane.

The SECOND AXILLARY SCLERITE, which is roughly quadrangular in shape, lies between the first axillary and the median plate. It is closely articulated above with the base of the radial vein to which it is partly fused. Viewed from the lower surface of the wing it is concave; it articulates with the alifer of the episternum.

The THIRD AXILLARY SCLERITE and the MEDIAN PLATE are fused into a single, strongly sclerotized, subtriangular plate. The base of this triangle articulates at one end with the posterior notal process and at the other with the base of the anal cell. Between these two points there is a small protruding flange to which strong muscles are attached.

The HUMERAL PLATE (hp) appears to be a sclerotization of the lower wing membrane only, although it is sometimes partly visible from above. It is a tiny triangular plate articulating between the base of the costa and the anterior

protuberance of the anterior basalare. The posterior protuberance of this basalare articulates with the base of the subcosta.

Two other secondary axillary sclerites are visible only in the lower wing membrane (Fig. 36); the *anterior subalare* and the *posterior subalare* (sub). The *anterior subalare*, which articulates with the second axillary sclerite, is the larger of the two. The *posterior subalare* is a very small sclerite situated close to the lower tip of the third axillary sclerite.

In the folding of the wing, the straight outer margin on the combination third axillary and median plate forms the major hinging surface. Reference to Figure 37 will make plain the mechanism of this folding process. By the use of muscles extending from attachment points within the body to the margin of the third axillary sclerite the straight outer margin of this sclerite is forced upward and over onto the dorsum of the insect through a wide arc. Since the anterior part of the wing base does not pass through this wide arc of space but pivots at the bases of the subcosta and radius, the wing must of necessity be forced posteriorly inward, and thus it comes to rest over the abdomen as the third axillary is folded back over the dorsum.

HIND WING.—The wing base of the hind wing is very similar to that of the fore wing in most details. A few minor modifications occur at the base of the anal veins due to the larger size of the anal area (vannus) in the hind wing.

WING VENATION

The venation of the genus *Capnia* (Fig. 17) is much reduced both in its longitudinal veins and in its crossveins. Those veins which are present are well developed and of nearly equal strength.

FORE WING.—The veins of the fore wing are well sclerotized and are dark brown in color except for the base of the cubitus which is weakly sclerotized.

The **COSTAL VEIN (C)** is simple, forming the anterior margin of the wing.

The **SUBCOSTA (Sc)** is a nearly straight vein which curves rather abruptly to enter the radius at the cord or just before reaching it.

The **RADIUS (R)** branches into R_1 and R_s shortly distad of its junction with media. R_1 is bowed strongly upward from the point of origin; in some cases the bend is as strong as the downward bending of R_s at this same point. R_1 is unbranched; R_s is once forked at or beyond the cord.

MEDIA (M) arises from the radial stem nearly at right angles to it. From a point of junction with the *arculus* the media extends as a simple vein to the cord where it forks to form M_1 and M_2 .*

The basal part of the **CUBITUS (Cu)** is very weakly developed. At its point of junction with the *arculus* or slightly proximad of this point it branches into two nearly straight veins, Cu_1 and Cu_2 .

* The *arculus*, as used here, is defined for convenience as the crossvein between the bases of M and Cu in the fore wing and between $R_s + M$ and Cu in the hind wing of Plecoptera.

The ANAL VEINS (A) are two in number, arising from the tiny *anal cell*. The *first anal vein* proceeds outward from the apex of the anal cell for a very short distance. At the cubito-anal crossvein it bends abruptly caudad and within another very short distance bends abruptly outward again. At this angular bend a heavy patch of sclerotization occurs. Most of it occurs above the vein and assumes a roughly triangular shape. A small amount of sclerotization occurs below the vein, however. The region of the anal veins is not developed into a *vannus* in the fore wing.

CROSSVEINS are few in *Capnia nigra*. The following primary crossveins are present: *humeral*, *radial*, *radio-medial*, *medio-cubital*, *arculus*, *cubito-anal*, and *anal*. Supplementary crossveins are 4 or 5 in number: one or two *costal*, one oblique crossvein in the marginal cell beyond the subcosta, one *median* and one *intercubital*.

The CORD is an oblique transverse line of bracing at the broadest part of the wing slightly distad of the middle. It is composed of *r*, *r-m*, *m-cu*, *cu* and the bases of M_1 and M_2 .

HIND WING.—The veins of the hind wing are well marked but not as darkly sclerotized as those of the fore wing.

The COSTAL VEIN (C) is unbranched, forming the costal margin of the wing.

The RADIUS (R) branches near its base into R_1 and R_s . R_1 is not bowed at the base as it is in the fore wing. R_s branches from R_1 at a sharp angle. It may branch into R_{2+3} and R_{4+5} either just after passing through the cord or just basad of it. In the latter case basal sections of R_2 and R_3 become part of the cord.

The base of MEDIA (M) joins the radius at an acute angle at a point slightly distad of the arculus. It branches into M_{1+2} and M_{3+4} some distance beyond the cord.

The CUBITUS (Cu) branches into Cu_1 and Cu_2 very near its base and shortly beyond *cu-a*.

An ANAL FAN (*vannus*) is present and is of considerable size in the hind wing. It extends distally to a point slightly beyond the cord or about two-thirds the distance to the wing tip.

The ANAL VEINS (A) are three in number. The *first anal vein* arises from the apex of the anal cell, curves slightly cephalad, and then proceeds along a nearly straight line to the wing margin. The *second anal vein*, which is nearly as long as the first, arises from the base of the anal cell. Arising from the same point is the much shorter *third anal vein*.

Primary CROSSVEINS are as in the fore wing; secondary or supplementary crossveins are fewer in number than in the fore wing since a secondary median crossvein is never present in the hind leg.

The CORD of the hind wing is similar to that of the fore wing except that

since media forks distad of the cord in the hind wing the bases of M_{1+2} and M_{3+4} do not enter into the composition of the cord.

LEGS

Figs. 31, 32

The legs (Fig. 31) are long and slender. The fore legs are the smallest, being slightly smaller than the mesothoracic legs which in turn are considerably smaller than the metathoracic legs. The differences in sizes of the legs is accounted for especially by differences in length of the femur, tibia, and tarsus since the coxa and trochanter are practically identical in size in all six legs.

The COXA (cx) or basal leg segment is moderately sized, appearing largest in sternal view. In anterior view the coxa is unmarked except for a narrow prearticular part of the basicoxite which is well delimited by the basicostal suture. No coxal suture is present. On the posterior surface of the coxa, however, is a suture that extends basad from the posterior trochanteral articulation (Fig. 31). Between the basal end of this suture and the trochantinal articulation a moderately large meron is demarked at the base of the coxa.

The TROCHANTER (tr) is a very short segment articulated with the coxa by an anterior and a posterior condyle. The deeply emarginate upper margin of the coxa allows for a wide range of motion of the leg on this dicondylic hinge. A dicondylic hinge is also present at the distal end of the trochanter. It operates in a plane at right angles to the distal coxal hinge, but permits of much less freedom of motion than the latter since nearly the entire distal rim of the trochanter is closely adjacent to the end of the femur.

The FEMUR (fe) is approximately twice as long as the coxa and trochanter combined. It is of nearly uniform width throughout its length. The sides of the femur are bounded ventrally by ridges running the length of the segment. These ridges delimit a concave ventral surface of the femur forming a groove for the reception of the tibia when the latter is flexed close against the femur.

The TIBIA (ti) is slightly longer and more slender than the femur. It is slightly compressed and nearly uniform in cross-section throughout its length. It is articulated to the femur by a dicondylic hinge. At its distal, lower margin it bears two diverging spurs.

The BASITARSUS is articulated to the tibia by a dorsal monocondylic hinge. It is a nearly cylindrical segment and is about three times as long as wide.

The SECOND TARSOMERE is of about the same diameter as the first but is very short, being only about one-fourth the length of the first tarsal segment to which it is closely articulated.

The THIRD TARSOMERE or DISTITARSUS, which is slightly longer than the first, is the longest of the three tarsal segments (except in the metathoracic legs where the first tarsal segment is the longest). It articulates loosely with the distal end of the second tarsal segment by means of a dorsal monocondylic hinge.

The PRETARSUS (Fig. 32) or terminal region of the leg consists of *claws*, *arolium*, *orbicula*, *basipulvilli*, and the *unguitractor*. The *claws* or *ungues* are the largest parts of the pretarsus. They both articulate with a small dorsal process (*unguifer*) of the last tarsal segment. From this point they diverge and curve downward to their sharply pointed apices. Ventrally their bases are connected with membrane which is also closely attached to the mesally located *unguitractor* (*ut*). The *unguitractor* is a ventral sclerite that can be retracted into the *distitarsus* by the action of muscles in the tibia that are attached to the *unguitractoral tendon* which in turn is attached to the proximal end of the *unguitractor*. Retraction of the *unguitractor* results in flexure of the claws. Located immediately below the claws and very close to the lateral distal angles of the *unguitractor* is a pair of setiform *basipulvilli* (*bp*). These are somewhat curved inward and are not as long as the claws. A median lobe, the *arolium* (*ar*), lies between the claws. This structure is largely membranous. Dorsally it is partly covered by a sclerotized plate called the *orbicula* (*or*). The *orbicula* expands distally and is slightly deflected over the sides of the *arolium*.

Abdomen

Figs. 42, 48, 49, 54, 55

The abdomen of Plecoptera is generally considered to consist of eleven segments, although interpretations as to the segmental distribution of the genitalia vary.

PREGENITAL ABDOMINAL SEGMENTS

Figs. 48, 49, 54

In the MALE of *Capnia nigra* the pregenital abdominal segments are eight in number. The tergal and sternal regions of all pregenital segments are entirely sclerotized. The tergal and sternal plates of the first abdominal segment are relatively small and are widely separated laterally by a pleural membranous region against which the hind coxae lie. The tergal and sternal regions of the remaining pregenital segments are separated by only a narrow strip of membranization which extends along the pleuron.

The FEMALE pregenital segments are seven in number. They are similar to those of the male except that a mid-dorsal membranous stripe of about one-third the width of the abdomen traverses all eight segments (Fig. 49).

MALE TERMINALIA

Figs. 42, 54, 55

The male terminalia of *Capnia nigra* involve abdominal segments nine, ten, and eleven. The posterior margin of the ninth tergite is conspicuously elevated to form a large median process (Fig. 54). The tenth tergite is divided into two rounded sclerites fused posteromesally to the basal bulb of the supraanal process. The *supraanal process* (*sa*) is a short recurved process.

On the sternum (Fig. 42), the ninth segment and the subanal lobes are

involved in genitalic modifications. The sternum of the tenth segment is not developed. A narrow basal rim of the ninth sternite is continuous laterally with the tergal sclerite. A small *ventral appendage* or *lobe* (*va*) is borne mesally on the basal rim. The major portion of the ninth sternite consists of a large rounded lobe or subgenital plate which is separated by membrane from all other sclerotized parts of the segment except at its lateral basal angles. Although it is usually not produced beyond the bases of the subanal lobes in the Capniidae, Klapalek (1896) has used the term subgenital plate for this structure. The *subanal lobes* (*sbl*) are sternal structures belonging to the eleventh segment. Proof of this is exhibited by other Plecoptera, such as the Perlodidae, wherein the tenth segment is a complete unmodified annulus anterior to the subanal lobes. They are small, roughly triangular sclerites which are closely adjacent to each other along their mesal edges. They are both joined mesally to an internal *fusion plate* (*fp*) which in *Capnia nigra* is two to three times as long as wide. It is widest near the base and tapers posteriorly to a slender apical region which extends beyond the subanal lobes. Anteriorly it is connected by membrane with a narrow, sclerotized, *retractor plate* (*rp*) to which strong muscles are attached. Klapalek (1896) has figured this entire structure in detail and has called it a titillator. However, since this same term has been applied to a different structure in Leuctra, I prefer to use the term *fusion plate* (*fp*). The *cerci* are borne in the membranous apical abdominal region on either side of the anus. They are 16-segmented in the male specimen studied.

FEMALE TERMINALIA

Figs. 48, 49

The female genital opening lies on the mid-ventral line between the margins of the eighth and ninth sternites. There are no external genitalic modifications except in the distal region of the eighth sternite, the hind margin of which has a slightly recessed area with a broadly arcuate margin (Fig. 48). The eighth tergite is membranized medially to form the distal end of the membranous stripe mentioned under the discussion of pregenital segments. The ninth segment is unmodified. The tenth segment is nearly as large as the ninth dorsally, but disappears ventrally. The *subanal lobes* (*sbl*) are subtriangular in shape and are slightly larger than those of the male. No median fusion plate, such as that which joins the subanal lobes of the male, is present. The *cerci* (*ce*), which lie on either side of the anus, are similar to those of the male and are composed of nineteen segments in the specimen studied. The *epiproct* (*epi*), or remnant of the dorsal part of the eleventh abdominal segment, which lies above the anus but below the protruding margin of the tenth tergite, is a very tiny sclerite.

Part II. Comparative Morphology of the Capniidae

ALLOCAPNIA Claassen

Figs. 18, 26, 35, 38, 38A, 45, 59

The following discussion on *Allocapnia* is based on a study of the genotype species, *Allocapnia granulata* (Claassen) and on all but three of our other North American species in this genus.

Several characters indicate that *Allocapnia* is a very specialized and homogeneous group of Capniidae. All of its species have a very marked tendency toward the atrophy of thoracic sutures. Its wing bases, anal fan, and male genitalia are distinctive also.

Its closest affinities seem to be with *Capnia* which it resembles somewhat in sternal thoracic characters, in the slight bend at the base of R_1 of the fore wing, in the ninth sternite and in other genitalic features of the male. The supraanal process of one species of *Capnia*, *C. spinulosa* Claassen, is identical with that of *Allocapnia* in its basic plan (elongate, bipartite, and with the lower prong grooved to form a sheath for the upper prong). As in *Capnia* there is a tendency toward brachyptery especially in the male sex. Brachyptery is considerably more advanced in some species than in others and often varies markedly in extent within a given species.

HEAD.—The head capsule and mouthparts of *Allocapnia* do not differ noticeably from those of *Capnia*, described in preceding pages.

THORAX.—All three thoracic segments differ significantly from those of *Capnia*. The pronotum is similar to that of *Capnia* but the meso- and metanota (Fig. 38) are considerably specialized by the fusion of most of the tergal plates and by other variations. The prealar bridge (pra), prescutum (psc), and scutum (sct) usually merge with one another to form a single irregularly shaped plate. The anterior notal wing process is somewhat protrusile and causes the displacement outward of the first axillary sclerite. The lateral edges of the scutum (sct) of both wing-bearing segments are deeply emarginate at a point opposite the third axillary sclerite. This modification is necessary to permit movement of the unusually large bundle of muscles extending from this sclerite to points of attachment within the thorax. The posterior notal wing processes and the postscutellum are poorly demarked from the scutum. The scutellum (scl) is well demarked, however.

The prothoracic pleuron of *Allocapnia* is like that of *Capnia*. The meso- and metathoracic pleura (Fig. 35), are different in several respects, however. The anterior basalare (ab) is united with the anterior margin of the posterior basalare (pb) and therefore is not capable of independent motion. Apparently as a compensatory mechanism, a small region of the apex of the posterior basalare is made moveable by the development of two lines of membranization extending inwardly from either side of the basalare. These two converging lines sometimes meet so as to demark completely a tiny apical sclerite. There is no suture demarking the anepisternum (aes) from the katapisternum (kes) in *Allocapnia*. The trochantin (tn) does not arise within the katapisternum (kes)

as it does in *Capnia* but arises at its lower margin. The spiracular sclerites are considerably larger than those of *Capnia*. There is no postalar bridge in either the meso- or metathorax.

The prosternum is like that of *Capnia* (Fig. 26). The mesosternum is also similar to that of *Capnia*, but differs in some respects. In *Allocapnia* the anterior angles of the basisternum do not bear digitate projections and are not joined to the apices of the arms of the spinasternum which lies anterior to it. The furcasternum is like that of *Capnia nigra* except that it is larger and the sternacostal suture demarking its anterior border is sometimes poorly developed. The postfurcasternal plates are never united to the spinasternum. In the metasternum no digitate projections occur at the anterior lateral angles of the basisternum as they do in *Capnia*. The furcal pits are widely separated and the sternacostal suture connecting them is sometimes so indistinct that a postfurcasternal sclerite is virtually undemarked.

WINGS.—The WING BASES of the meso- and metathorax are similar to each other but are considerably different from those of *Capnia*. The differences can be understood best by a comparison of Figures 37 and 38. In *Allocapnia* the tegula is unusually large; the humeral plate is merely a tiny remnant; the first axillary sclerite is displaced outward by the protruding anterior notal process; the third axillary sclerite is notable for the tremendous development of its muscle flange especially in the hind wing; a very tiny accessory sclerite occurs between the base of the anal cell and the posterior angle of the third axillary sclerite in the fore wing but not in the hind wing.

An interesting condition occurs in the males of one species of *Allocapnia*, *A. vivipara* (Claassen), (Fig. 38A) in which there are almost no wings at all. The wings are so reduced as to be much smaller even than the wing pads of a normal, full-grown naiad. The axillary sclerites, however, are of nearly normal size although they have undergone some modifications. The first axillary sclerite of the fore wings is fused at its posterior end with the scutum; and the posterior end of the third axillary is fused to the posterior notal wing process (pnp). In the metathorax the fusion of these sclerites is greater, and in addition, the three axillary sclerites are partially fused together. The tegula (tg) is large, and is fused to the prealar bridge (pra) and to the scutum (sct) in both meso- and metathorax.

WING VENATION of both fore and hind wings of *Allocapnia* is basically similar to that of other Capniidae (Fig. 18). It differs, however, in a few very significant details. Even in specimens with well developed wings the region of the wing beyond the cord is relatively small, and the subcosta ends considerably basad of the cord. R_1 of the fore wing is bent upward slightly at its origin but not to the extent of the arcuation of this vein in *Capnia*; 1st A is straight. In the hind wing, media is usually unbranched and in some species is atrophied basally or absent entirely; Cu is unbranched.

The simple unbranched condition of Cu in the hind wing is due apparently to the complete atrophy of Cu_1 in this genus. Intermediate stages of brachyptery are exhibited in *Paracpnia* where the apical section of Cu_1 beyond m-cu

is almost always absent. Okamoto's (1922) figure of the hind wing of *Takagripopteryx* shows a condition of Cu_1 like that of *Paracapnia*. The partial brachyptery of Cu_1 in these two genera is a strong indication that *Alloicapnia* (a closely related genus) has acquired its unbranched cubitus by the complete atrophy of Cu_1 .

The vannus extends considerably beyond the cord and is nearly as large as the rest of the wing; its venation, however, is similar to that of *Capnia*.

LEGS.—The legs are similar to those of *Capnia*.

ABDOMEN.—Abdominal features of *Alloicapnia* are similar to those of *Capnia nigra* except as they are involved in specific modifications.

The PREGENITAL SEGMENTS of the male sex vary in number among the species of *Alloicapnia* from 5 to 7 depending on the number of segments exhibiting genitalic modifications. The tergal and sternal regions are entirely sclerotized and are separated by only a narrow strip of membranization which extends along the pleuron. All pregenital segments of the female sex are traversed mid-dorsally by a membranous stripe of about one-half the width of the abdomen.

The terminalia of the male sex of *Alloicapnia* involve from four to six apical abdominal segments. The sixth, seventh, and eighth or the seventh and eighth or only the eighth tergite may bear sclerotized protuberances. The ninth and tenth tergites are always membranous. The supraanal process is a large, elongate, dorsally recurved, bipartite structure which lies over the membranous portions of the ninth and tenth tergites. The lower branch of this process is grooved and serves as a sheath for the upper portion through which the genital products are discharged.

The basal region of the ninth sternite is continuous laterally with the pleural region (Fig. 45). The ninth sternite bears no ventral appendage. The subgenital plate (sbp) merges with the basal portion of the segment: it is strongly demarked laterally from a relatively broad membranous region. Apically it bears a small nipple. The fusion plate of the subanal lobes in *Alloicapnia* is two or three times as broad as that of *Capnia* at its base (Figs. 59, 60). It tapers only slightly for most of its length; near the apex it narrows abruptly to a small, downwardly hooked, apical process. The retractoral plate (rp) is small and transverse in *A. pygmaea* and in several other species, while in *A. recta* it is sagittally elongate.

The genitalia and terminalia of the female sex are basically similar to those of *Capnia*. In some species the eighth tergite is membranized dorsally and forms the posterior end of the dorsal membranous stripe.

CAPNIA Pictet

Figs. 1-3, 5-10, 17, 25, 31-33, 36, 37, 42-44, 48, 49, 54-58

Since several anatomical features of *Capnia* exhibit a considerable amount of variation among the numerous species of this genus, further notes concerning the entire genus are necessary to supplement the discussion of *Capnia nigra* contained in the preceding pages.

The following discussion of *Capnia* is based on a study of the genotype species, *Capnia nigra*, and upon another European and nearly all known American species of this genus. A list of the names of all of the species studied is included in a table at the end of this article.

It seems probable that *Capnia* is still an actively evolving genus since structures that offer excellent and constant generic differences in other genera exhibit wide ranges of variation in *Capnia*. There appear to be at least three intergrading subgroups within the genus.

HEAD.—Neither the cranium nor the mouthparts appear to vary noticeably among the species of *Capnia* studied.

THORAX.—In general, the only thoracic sclerites that exhibit variations within the genus *Capnia* are those of the mesosternum. As was noted under the discussion of *Capnia nigra*, however, a strongly brachypterous condition of the male is associated with a merging of certain usually well demarked tergal and pleural regions of the pterothorax.

With but one exception known to me the wings of our North American species of *Capnia* are not atrophied sufficiently to be accompanied by the merging of thoracic sclerites. The completely wingless male of *Capnia fibula* Claassen exhibits tergal and pleural modifications of the meso- and metathorax (Fig. 39) that are as remarkable as any that are to be found in the entire genus. The region normally occupied by the axillary sclerites and by the tegula is completely and uniformly sclerotized. This region merges with the scutum (sct), the prealar bridge (pra), and the posterior notal wing process (pnp) but not with the anterior notal wing process (anp) which is distinctly visible. That this area contains, and is principally composed of, the three axillary sclerites and the tegula is indicated by the condition existing in *Allocaupnia vivipara* (see discussion under *Allocaupnia* and Fig. 38A) where a less complete fusion of these sclerites has taken place.

Other interesting modifications accompany the brachyptery of the male of *Capnia fibula*. Only a small section of the suture that demarks the scutellum from the scutum is present. In the pterothoracic pleura also the anterior and posterior basales and the alifer fuse into a single, apparently nonfunctional process. The mesothoracic furcasternum varies from a roughly semicircular shape in *Capnia nigra* (Fig. 25) and a few other species of *Capnia* to the transverse shape shown in Figure 33. In a few species the postfurcasternal plates are united mesally with the spinasternum and also lie closely adjacent to, but are not united with, the furcasternum. This condition is often associated with a bipartite condition of the supraanal process of the male.

WINGS.—The wings of all species of *Capnia* are identical with those of *C. nigra* (Fig. 17) except for minor variations in numbers of crossveins and in the course of the first anal vein. In one species, *Capnia venosa* (Banks), there are usually one or more crossveins beyond the cord between R_1 and R_2 . In many species the bend at the base of the first anal vein of the fore wing is slight and no patch of sclerotization occurs at this bend. All stages of intergradation between this condition and that of *Capnia nigra* where both the angular bend

of the first anal vein and the triangular patch of sclerotization are well developed occur among the species of *Capnia*.

ABDOMEN.—Abdominal features of *Capnia* vary considerably since several segments may be involved in genitalic modifications especially in the male sex.

The PREGENITAL SEGMENTS of the male sex vary in number among the species of *Capnia* from three to eight, depending on the number of segments exhibiting genitalic modifications. As in *Capnia nigra* the tergal and sternal regions of all pregenital segments are entirely sclerotized. The first five or six tergites are sometimes divided into two laterotergal plates by a moderately broad band of membranization when none of these are modified into genital segments.

The pregenital segments of the female are identical to those of *Capnia nigra* (Fig. 49) except in a few species of *Capnia* in which the first one or two abdominal tergites are not membranized mesally.

The MALE TERMINALIA of *Capnia* involve from three to eight distal abdominal tergites depending on the species concerned. In only one known species do the fourth, fifth, and sixth tergites bear sclerotized protuberances. In numerous cases the seventh tergite alone bears protuberances of various shapes and sizes. In such cases the eighth and ninth tergites are usually membranous dorsally. In other species only the eighth tergite bears protuberances. Dorsal processes rarely occur on the ninth segment. Sometimes no tergal genital structures except the supraanal process occur. It is always recurved over the abdomen and may assume various forms varying from a greatly attenuate type to a markedly bulbous type. It is usually unipartite but is sometimes bipartite and variously shaped.

On the sternum, only the ninth sternite and the subanal lobes are involved in genitalic modifications. The basal region of the ninth sternite is continuous laterally with the pleural region, as in *Capnia nigra* (Fig. 42). This basal region varies considerably in size among the species of *Capnia* studied (Figs. 43, 44) but is usually at least twice as broad as that of *Capnia nigra*. Some species, particularly the more northern ones such as *C. nearctica* Banks, have a subgenital plate which is very similar to that of *Allocaenia* (Fig. 45). Perhaps the most remarkable difference between *C. nigra* and all other species of *Capnia* is the entire absence of a ventral lobe and the complete fusion of the subgenital plate to the basal region of the segment (Figs. 43, 44) in all species except *C. nigra*. The median nipple at the apex of the subgenital plate shows some specific difference of shape.

The fusion plate of the subanal lobes of *Capnia* exhibits a considerable amount of variation. In many species it is much broader than in *Capnia nigra* (Fig. 56). In at least one species of *Capnia*, *C. fibula* (Fig. 57) the fusion plate is narrower than that of *C. nigra* and its retractoral plate is long and subulate.

The FEMALE TERMINALIA are similar to those of *Capnia nigra* (Figs. 48, 49) except for specific variations in the eighth sternite which is rarely if ever protrusile or bipartite.

CAPNIONEURA Ris

Figs. 4, 11, 19, 27, 46

Fortunately I have had the opportunity of studying the genotype species of *Capnionemura nemuroides*, at the Museum of Comparative Zoology of Harvard University. The specimens studied were identified by Ris himself, and they agree perfectly with his description and figure of the male (1913) and of the female (1905).

The elongate wings, the long straight veins, the absence of costal crossveins, and the short cerci indicate a closer relationship with *Nemocapnia* and *Eucapnopsis* than with other genera of Capniidae. The above-mentioned characters and several features of the male genitalia seem to indicate affinities with the Leuctridae also.

Indeed, certain features exhibited by *Capnionemura* provoke a considerable amount of doubt as to the advisability of recognizing the Leuctridae and the Capniidae as families distinct from each other. In some features, particularly of the male genitalia, *Capnionemura* is definitely more similar to *Paraleuctra* and *Megaleuctra* (Leuctridae) than to any Capniid genera. However, if the Capniidae and Leuctridae are to be recognized as distinct families, the genus *Capnionemura* must be assigned to the Capniidae because of its numerous affinities with other genera of this family.

HEAD.—In certain features of both the head capsule and the mouthparts *Capnionemura* differs very significantly from all other Capniidae. The frons is completely divided into two parts by a suture immediately in front of the median ocellus. As was suggested under the discussion of the frons of *Capnia nigra*, the anterior portion of the head capsule that is delimited by this suture may possibly constitute the entire true frons. The distance between the lateral ocelli is nearly five times the distance of either ocellus from the compound eye nearest to it. Postfrontal sutures are entirely lacking but the coronal suture is distinctly visible in the posterior region of the head.

One of the most interesting modifications of the cranium of *Capnionemura* concerns the anterior tentorial pits (Fig. 4). In all other genera of Capniidae they assume the form and position as described in detail for *Capnia nigra* on a previous page. In *Capnionemura* the anterior tentorial pits are not continuous with the anterior border of the antennal socket. Each anterior tentorial pit is visible externally as a curved suture which is laterally continuous with the hypostomal suture. It passes in front of the antennal socket and meets the antennal suture at a point near the ventral antennifer. The curved plate or region of the head capsule which is bounded by this suture and by the antennal suture merges with the frons.

The labium (Fig. 11) differs from that of *Capnia* in several important respects. The paraglossae (pgl) are large, and each is demarked at its base by a diagonal sclerotic rim or bar. Nearly the whole distal half of the labiostipites (lbi) is membranous. The lateral distal angles of the submentum (sm) bear sclerotized points that articulate with the mentum (mn).

THORAX.—The thorax of *Capnioneura* (Fig. 27) differs from that of *Capnia* principally in sternal characters of the meso- and metathorax. Less significant differences also occur in the pronotum and in the meso- and metathoracic pleura.

A precosta is not demarked in the pronotum. In the meso- and metathoracic pleura the demarcation between the anepisternum and the katepisternum is very indistinct but is similar to that of *Capnia* in other respects. The demarcation between the pleuron and the sternum is distinct and the base of the trochantin does not encroach on the katepisternum.

The prothoracic sternum of *Capnioneura* differs from that of *Capnia* principally in the furcasternum which is more transverse in *Capnioneura* than in *Capnia*. The mesothoracic furcasternum is small, strongly transverse and split along the mid-ventral line by a distinct suture. The postfurcasternal plates of the female specimen studied are fused on three sides to the spinasternum, furcasternum, and furcasternal arms. In the male specimen which I studied the furcasternal plates are separated from the furcasternal arms by a narrow intervening membranous region. The furcal pits of the metathorax are about as far apart as are those of the mesothorax. The metathoracic furcasternum is narrow, transverse, and united with the first abdominal sternite.

WINGS.—The wing bases and venation (Fig. 19) are similar to those of *Capnia* in most details but differ significantly in some. The subcosta is straight and runs into the costa at the cord. A crossvein extends between R_1 and the apex of Sc. There are no other costal crossveins either before or beyond the tip of the subcosta. R_1 of the fore wing is not bent at its origin. The first anal vein of the fore wing is straight. The anal fan of the hind wing extends beyond the cord but is not as broad as that of *Capnia* and is small in size relative to the size of the rest of the wing. The venation of the anal fan is considerably different from that of *Capnia* in possessing four anal veins two of which arise at separate points at the apex of the anal cell and the other two of which arise from separate points at the base of the anal cell. The first three are long and straight; the fourth is less than one-half the length of the third.

ABDOMEN.—The abdomen of *Capnioneura* is very interesting because of its numerous unique features and its affinities with both the Capniidae and the Leuctridae.

The PREGENITAL SEGMENTS of the male sex are eight in number. Both the tergites and the sternites of all segments except the first are completely sclerotized. The first abdominal tergite is mostly membranous.

The pregenital abdominal segments (7 in number) of the female are notable for the lack of sclerotization. The tergites of each of these segments is represented only by a pair of small, pleurally located plates. Each pregenital sternite bears a single median plate which covers only about half of its segment.

Several features of the MALE TERMINALIA are particularly noteworthy (Fig. 46). The ninth tergite is unmodified. The tenth tergite is not divided into two

rounded lobes as in other Capniidae but forms a continuous transverse sclerite. The supraanal process is a short, upwardly directed, posteriorly grooved structure strongly resembling that of *Megaleuctra* and *Paraleuctra* (Leuctridae). The ninth sternite bears no ventral appendage. Its subgenital plate more strongly resembles that of *Paraleuctra* than that of any Capniid genus. It is produced under the subanal lobes, bears no nipple at its apex, and is not demarked laterally by a distinct suture although it is partially demarked from the rest of the ninth sternite by regions of membranization. The subanal lobes are remarkably different from those of other Capniid genera but are identifiable as being of the Capniid type by their conspicuous fusion plate.

The subanal lobes are of an extremely specialized type. Each consists of two separate, very narrow and elongate sections. The basal section is attached, as usual, at the lateral angles of the tenth tergite. It extends anteriorly for a short distance and then curves mesally to meet at a mid-ventral point with the base of the distal section of the subanal lobe and with the fusion plate. The distal sections of the subanal lobes lie parallel to each other along a sagittal line. In ventral view they appear nearly straight and are of uniform width for most of their length but taper to a pointed apex. In lateral view they appear to curve gently upward. The length of the fusion plate is about half the length of the median sagittal portions of the subanal lobes. From a bulbous region near its base a narrower projection extends posteriorly to an apex which appears blunt in ventral view. In lateral view, the bulbous portion lies dorsad of the lobes. Apically it is deflected at a right angle bend so as to project down between the subanal lobes. Each cercus is composed of a single segment. This segment bears a flap that curves around its inner surface and partly covers its dorsal surface. What appears to represent the remainder of a second segment occurs as a very tiny button at the apex of the cercus.

Of the FEMALE TERMINALIA the eighth and ninth tergites, like the pre-genital tergites, are membranous. The eighth tergite bears a small median sclerotized plate similar to that found in some Leuctridae (*Paraleuctra*). The tenth tergite is completely sclerotized. The seventh and eighth sternites are mesally fused. The eighth sternite is slightly produced and slightly cleft. The ninth sternite is completely sclerotized. The subanal lobes are unmodified. The cerci are 1-segmented and each bears a tiny nipple (probably segment two) apically. The eighth sternite of *Capnioneura nemuroides* Ris, as described above, is similar to that of *Paraleuctra*, but that of *C. brachyptera*, as described by Ris (1932) is neither produced nor cleft.

CAPNOPSIS Morton

Figs. 12, 20

I have been very fortunate in obtaining a specimen of this genus for study. Quite by accident, I discovered a single female in the Cornell Collection bearing the label *Allocapnia pygmaea*. Although it is not a well preserved specimen it is unquestionably a *Capnopsis*. As might well be suspected from a study of the excellent figures of the wings published by Rostock in 1892 it is a very interesting and specialized genus of Capniidae. In many ways it appears to be

quite unique; but in several of its features it bears resemblances to various other genera of Capniidae.

HEAD.—The head capsule is basically similar to that of other Capniidae but resembles *Paracapnia* in particular in the entire absence of a coronal and of postfrontal sutures. The antennae are short (15-segmented) and appear to be nearly glabrous. The labium (Fig. 12) differs from that of *Capnia* and other Capniid genera in several respects. When extended forward, the palpi project considerably beyond the glossae and paraglossae. The paraglossae, as well as the glossae, are demarked at their bases by transverse, sclerotic rims. The labiostipites is not distinctly divided into a distal membranous region and a sclerotized basal region. The mentum appears to merge at its lateral angles with the submentum.

THORAX.—The proportionate sizes of the thoracic segments is considerably different from other Capniid genera except in the sternum. The pronotum is noticeably more transverse than in other genera, and the metathoracic pleura and terga are also markedly shorter.

The pronotum is not split by a mid-dorsal suture, and, as mentioned above, it is markedly transverse. The postscutellum of the mesothorax is relatively large but otherwise is practically unmodified. The metathoracic tergum is considerably shortened as a result of which its demarked regions are exceptionally transverse.

The thoracic pleuron, except for proportionate sizes in the metathorax is very similar to that of *Capnia*. There is no postcoxal bridge in the prothorax, however. The mesothoracic trochantin encroaches on the katepisternum slightly more than in *Capnia*; the trochantin of the metathorax does not encroach on the katepisternum of this segment at all.

The sternum is very similar to that of *Capnia* but differs in a few important details. In the prosternum a postcoxal bridge is absent and the apices of the arms of the spinasternum are not united with the lateral anterior angles of the mesothoracic basisternum although the latter sclerite and the basisternum of the metathorax bear digitate projection at their lateral anterior angles. The mesothoracic furcasternum is very small, triangular, and free from the furcasternal plates. The metathoracic furcasternum is united with the first abdominal sternite.

WINGS.—The wings of *Capnopsis* (Fig. 20) are extremely interesting and remarkable for the amount of reduction which they exhibit. Most of the principal remigial longitudinal veins are present but the vannal region is extremely reduced.

FORE WING.— R_1 is straight; R_s leaves R at nearly a right angle; it is once forked at the cord. M is two branched. Cu is two or three branched. Rostock (1892) figures Cu as arising from the base of the anal cell. This is true in the hind wing of the specimen that I have studied but not in the fore wing. 1st A is short and nearly straight. 2nd A is entirely absent. All of the primary crossveins except $m-cu$ are present. No accessory crossveins are present in the costal area. The accessory crossvein between M and Cu_1 and the one which lies opposite it between Cu_1 and Cu_2 are both present.

HIND WING.—The remigium of the hind wing is short and unusually broad. Its venation is similar to that of the fore wing except that R_s is unbranched and an accessory costal crossvein occurs basad of the tip of the subcosta in one of the wings studied. The anal area is remarkably reduced; nothing remains of it except the anal cell to which, peculiarly enough, the base of Cu is joined. That the vein I am considering to be Cu_2 in this case (Fig. 20) is correctly identified seems certain since the crossvein that occurs between Cu_1 and Cu_2 is one of the most constant features of the Capniidae.

ABDOMEN.—The first abdominal tergite is mostly membranous. Tergites two through eight are traversed by a membranous band which is about one-third the width of the abdomen. The ninth and tenth tergites are completely sclerotized. All abdominal sternites appear to be completely sclerotized. The eighth sternite and the subanal lobes are practically unmodified. According to Morton the cerci are from seven to ten segmented.

EUCAPNOPSIS Okamoto

Figs. 13, 21, 28, 47, 63

My work on this genus is based on specimens of our North American species, *E. brevicauda*, which fit Okamoto's original generic definition so well that there can be hardly any doubt as to the correctness of its generic assignment. I have not seen specimens of the genotype species.

As was previously noted, this genus is closely related to *Capnioneura* and *Nemocapnia* for several reasons.

HEAD.—The cranium and all of the mouthparts except the labium of *Eucapnopsis* (Fig. 13) are similar to those of *Capnia*. The labial palpi of this genus are considerably longer than those of *Capnia* and thus when extended anteriorly they project considerably beyond the distal ends of the glossae and paraglossae. The labial palpi of *Eucapnopsis* are interesting also for a sexually dimorphic feature which they exhibit. In the female sex the second and third segments are about equal in length, the second being the thickest one. In the male the apical segment is much longer (often twice as long) and larger than the antepenultimate one, giving to the palpi a club-shaped appearance. In both sexes the third or apical segment is always at least twice as long as wide. The glossae and paraglossae are similar to those of *Capnia* but a considerably larger distal portion of the labiostipites is membranous than is the case in *Capnia*. The lateral angles of the submentum merge with the mentum but in the central region the two sclerites are separated by a broad V-shaped suture.

THORAX.—The thoracic tergum of *Eucapnopsis* is virtually identical to that of *Capnia* but certain significant differences occur in the pleural and sternal regions.

In *Eucapnopsis* there is a distinct postalar bridge not only in the metathorax but in the mesothorax. In neither wing-bearing segment does the trochantin encroach on the katapisternum.

Thoracic sternal differences are few but very distinct (Fig. 28). In the

prothorax the postcoxal bridge is not complete. It lies free as an indistinct curved sclerite not attached either to the epimeron or to the basisternum. The mesothoracic furcasternum is relatively small, narrowly transverse, and slightly curved. The postfurcasternal plates are not united with it or with the spinasternum.

WINGS.—The wings of *Eucapnopsis* (Fig. 21) differ considerably from those of *Capnia* but are very similar to those of *Capnioneura* and especially to those of *Nemocapnia*. R_1 of the fore wing is not bowed at its base. The number of accessory costal crossveins basad of the tip of the subcosta varies from one to four but is usually two or three. A costal crossvein beyond the tip of the subcosta is nearly as frequently absent as present. The first and second anal veins of the fore wing are straight. The anal fan of the hind wing extends slightly beyond the cord and is relatively small in area. The first and second anal veins of the hind wing are long and straight; the third is an extremely short and inconspicuous vein.

ABDOMEN.—The abdomen of *Eucapnopsis* is generally rounded above and flattened below.

The PREGENITAL SEGMENTS of the male sex are eight in number. The first five tergites are traversed mid-dorsally by a very narrow and indistinct membranous line. The remaining pregenital tergites and all of the pregenital sternites are completely sclerotized.

The pregenital tergites of the female are traversed by a mid-dorsal membranous stripe which is about one-third the width of the abdomen. The sternites are completely sclerotized.

MALE TERMINALIA.—The tergal sclerites are unmodified except for the tenth tergite, which as in *Capnia*, is divided into two rounded portions. The supraanal process of the species studied is small and bulbous. The ninth sternite of the male differs considerably from that of other genera of Capniidae (Fig. 47). The subgenital plate is separated from a narrow basal rim except at its lateral angles by a membranous region. The basal rim bears a median appendage which is about one and one-half times as long as wide and is beset with numerous heavy setae. The subgenital plate is about as broad as long; a narrow marginal area is demarked on each side near the apex; a small nipple is borne at the tip. The subanal lobes are subtriangular in shape. Their fusion plate (Fig. 63) is about two and one-half times as long as broad, is broadest at the base, and protrudes beyond the subanal lobes in the form of a very strongly compressed, knife-like process. Anteriorly it terminates in a broadly rounded lobe and it does not possess a retractoral plate. The cerci are very short and are composed of four or five segments.

FEMALE TERMINALIA.—The posterior end of the dorsal membranous stripe is formed by membranization of the eighth tergite. The ninth and tenth tergites are completely sclerotized. The sternites seem to exhibit no generic characters. The cerci, like those of the male, are four to five segmented.

ISOCAPNIA Banks

Figs. 14, 22, 29, 50, 64

The following discussion of the morphology of *Isocapnia* is based on a study of types and other specimens of *I. grandis* and *I. integra*.

It is difficult to determine the generic affinities of *Isocapnia* since it does not closely resemble any particular Capniid genus but seems to bear a few points of resemblance to the members of almost every genus of Capniidae. In the length of the labial palpus and its third segment it resembles *Eucapnopsis*. In the basal demarcation of its paraglossae it resembles *Capnionera*. In the union of its presternites with the corresponding basisternum and in its pterothoracic epimera it resembles *Nemocapnia*. In its male genitalia and cerci it resembles *Capnia*. However, by its usual large size and its peculiar combination of body and wing characters it can be distinguished easily from all other Capniid genera.

HEAD.—The cranium is similar to that of other genera of Capniidae except that a coronal suture is usually present and the parietal region is relatively large in *Isocapnia*. The labium (Fig. 14) resembles *Eucapnopsis* in that its palpi, when extended anteriorly, projects beyond the ends of the glossae and paraglossae and in that the third segment is about as long as the second. It differs from *Eucapnopsis* in that the mentum and submentum are completely separated from each other.

THORAX.—The thoracic tergum is similar to that of *Capnia* except in the highly variable suturing and coloration of the postscutellum.

The pterothoracic pleura are similar to those of *Capnia* in all but the following details. In both segments a postalar bridge is present. The demarcation between pleuron and sternum is complete. The base of the trochantin does not encroach upon the katapisternum. The mesothoracic epimeron bears a transverse, darkly colored, and slightly depressed region. In the corresponding position of the metathoracic epimeron is a dark patch. These areas, as in *Nemocapnia*, apparently represent the beginnings of a division into anepimeron and katepimeron.

The sternum (Fig. 29) is very distinctive but somewhat resembles that of *Nemocapnia* from which it differs in the following respects. The prothoracic furcasternum is larger and not so narrow as that of *Nemocapnia*. Its sternocostal suture is incompletely demarked. In some specimens of *I. grandis* this furcasternum is produced posteriorly at two points to unite with the postfurcasternum. The mesothoracic presternum is larger than that of *Nemocapnia*. The furcasternum, spinasternum, and postfurcasternal plates of this segment are united to each other. The furcasternum is transverse; its posterior margin is sometimes only indistinctly demarked from the furcasternal plates. The furcasternal arms are united with the postfurcasternal plates in some specimens but not in others. The metathoracic presternum is large and partially divided secondarily into two transverse sections. The furcasternum of the metathorax is a large, transverse, rectangular sclerite which is only very poorly demarked from the first abdominal sternite with which it is united.

WINGS.—The wings (Fig. 22) are large and not as slender as in *Nemocapnia* or *Eucapnopsis*. Costal crossveins basad of the tip of subcosta are one to five in number; those beyond the apex of the subcosta vary from none to three in number. R_1 and 1st A of the fore wing are straight at the base. The radial sector of the fore wing may fork in the cord or beyond it and may be two to four branched. The vannus of the hind wing is similar to that of *Capnia* in both size and venation.

ABDOMEN.—The PREGENITAL SEGMENTS of the male are eight in number. Both the tergites and the sternites of all segments are completely sclerotized.

The pregenital sternites of the female are completely sclerotized. The first abdominal tergite has a large, transverse, membranous area. The remaining pregenital segments are traversed by a mid-dorsal membranous stripe which is only one-fourth to one-fifth the width of the abdomen.

MALE TERMINALIA.—The ninth tergite is unmodified. The tenth tergite is divided into two rounded portions which unite posteromesally with the bulbous base of the supraanal process. The supraanal process is a recurved, usually elongate structure. The ninth sternite (Fig. 50) is completely divided into two separate parts. The relatively small, transverse, basal portion articulates laterally with the subgenital plate and the posterior angles of the decurved ninth tergite. Mesally this irregularly shaped plate bears a conspicuous ventral appendage which is very narrow at the base and of nearly one-third the width of the abdomen near its apex. The subgenital plate is well demarcated on all sides from surrounding sclerotized regions. Its apex bears no nipple. The subanal lobes are roughly triangular in shape. Their fusion plate (Fig. 64) is extremely elongate. It extends for a considerable distance beyond the apices of the subanal lobes as two very slender, sharply pointed processes which are joined together for most of their length. To its base, which is bulbous, is attached an extremely long, subulate, retractoral plate. The cerci of all the specimens studied are broken. One specimen has a cercus of 13 segments and appears to have had probably 20 or more.

FEMALE TERMINALIA.—The seventh and eighth tergites are split by the posterior end of the dorsal membranous stripe. The ninth and tenth tergites are completely sclerotized. The median posterior region of the eighth sternite is sometimes recessed but is never produced. The ninth sternite is completely sclerotized. The subanal lobes are unmodified. The cerci are most probably many-segmented like those of the male.

NEMOCAPNIA Banks

Figs. 15, 23, 30, 34, 51, 65

This discussion and the supplementing figures of *Nemocapnia* are based on specimens of *N. carolina* Banks that were carefully checked against the three type specimens of this species at the Museum of Comparative Zoology.

Wing venational features and certain prosternal structures ally this species closely with *Eucapnopsis*. Certain sternal and pleural features ally it with *Capnia*. Features of the labium, male genitalia, cerci, and of the thoracic ster-

num and pleuron easily distinguish *Nemocapnia* from all other genera of Capniidae.

HEAD.—The cranium and all of the mouthparts of *Nemocapnia* except the labium are similar to those of *Capnia*. The labium of *Nemocapnia* (Fig. 15) differs from that of *Capnia* in the following respects. The labiostipites is unusually large but its distal membranous region is rather small. The mentum is completely separated from the labiostipites and from the submentum by membrane. The lateral distal angles of the submentum bear sclerotized points which articulate with the mentum.

THORAX.—The thoracic tergum of *Nemocapnia* is identical to that of *Capnia*.

The pleuron is also very similar to that of *Capnia* even as to the incompleteness of the suture demarking the pleuron from the sternum and the encroachment of the bases of the trochantins of both pterothoracic segments upon the katepisternum. It differs from *Capnia* in having a transverse groove on the epimeron (Fig. 34). This groove is very distinct in the mesothorax and less distinct in the metathorax. It appears to correspond to the line of division of the epimeron into anepimeron and katepimeron. This is particularly noteworthy since, to my knowledge, such a division occurs in no other stonefly except the closely related *Isocapnia*.

The thoracic sternum (Fig. 30) is considerably different from the sternum of all other Capniidae in its combination of diagnostic characters. The lateral cervical sclerites are fused posteriorly to the precoxal bridge of the prothorax. The presternum is not separated from the basisternum. The furcasternum is a small, narrow, transverse sclerite. The postfurcasternum is an oval sclerite with a tendency toward membranization mesally. The spinasternum is fused at its apices with the anterior lateral angles of the mesothoracic basisternum. The postcoxal bridges of the prothorax are incompletely formed, being composed merely of a small sclerite that lies behind each coxa.

The mesothoracic presternum is not separated from the basisternum. The lateral posterior angles of the basisternum are continuous with the katepisternum. The furcal pits are widely separated. The furcasternum is a well defined, narrowly transverse sclerite. The spinasternum is of an unusually narrow elongate shape and is united with the posterior mesal point of the furcasternum. The postfurcasternal plates are large and are united closely with the spinasternum and furcasternum.

The metathoracic presternum is large and triangular in shape. Its posterior mesal angle merges with the basisternum. The basisternum is considerably shorter than that of the mesothorax. It bears finger-like projections at its anterior lateral angles, and merges at its posterior lateral angles with the katepisternum. The furcal pits of this segment are even more widely separated than those of the mesothorax. The furcasternum is a narrowly transverse, arched sclerite which is not united with the first abdominal sternite.

WINGS.—The venation (Fig. 23) of the hind wing is virtually identical to that of *Eucapnopsis*. The venation of the fore wing is more like that of

Capnioneura than that of *Eucapnopsis*. It resembles *Capnioneura* in the straight subcosta which runs into the costa and in the absence of supplementary costal crossveins except for the occasional occurrence of one crossvein basad of the tip of the subcosta. It may be distinguished from either of the above-mentioned genera by the anal veins. The first anal vein is slightly bent just beyond cu-a as in *Capnia*. The second anal vein curves abruptly near its apex to enter the margin of the wing at an angle of nearly 90° .

ABDOMEN.—The PREGENITAL SEGMENTS of the male sex are eight in number. Both the tergites and the sternites of all segments are completely sclerotized.

The pregenital segments of the female are similar to those of *Eucapnopsis*.

MALE TERMINALIA.—The ninth tergite of the single known species bears two slightly raised knobs. The supraanal process is an elongate, recurved prolongation arising from a large basal region which is closely united with the two halves of the tenth tergite. The ninth sternite bears no ventral appendage (Fig. 51). Its undifferentiated basal region is relatively large. A subgenital plate is demarked by a distinct suture but it is not separated laterally from the rest of the sternite by membranization. The subanal lobes are roughly triangular in shape. Their fusion plate (Fig. 65) is pyriform and apically is produced into a strongly depressed, slightly decurved process. It has no anterior extension (retractorial plate). The cerci are composed of six or seven segments.

FEMALE TERMINALIA are similar to those of *Eucapnopsis*.

Paracapnia gen. nov.

Figs. 16, 24, 40, 41, 52, 53, 66

This genus includes the species *opis* (Newman) and *curvata* n. sp. The erection of a new genus for these two species is necessary since they exhibit numerous features that will not permit of their being assigned to any other Capniid genus.

HEAD.—The head capsule and mouthparts are similar to those of *Capnia* and other Capniidae but differ in at least two important respects. The coronal and postfrontal sutures are entirely lacking, as in *Capnopsis*; and the paraglossae of the labium (Fig. 16) are usually narrower and never broader than the glossae. A distal membranous region of the labiostipites is not distinctly demarked from the more sclerotized basal region. The palpi, when extended forward, reach about to the tips of the glossae and paraglossae.

THORAX.—The thoracic tergum is very similar to that of *Capnia*. The pronotum differs in having no mid-dorsal pronotal suture and in that the lateral cervical sclerites are not united with the precoxal bridge.

The pterothoracic pleura differ from those of *Capnia* in some respects. In *Paracapnia* a demarcation between anepisternum and katepisternum is absent except for a slight indication of it anteriorly. The demarcation between the pleuron and the sternum of these two segments is very weak and incomplete. A postalar bridge is present in both segments.

The prosternum (Fig. 40) is nearly identical to that of *Capnia* but the pterothoracic sternum is quite distinct from that of any other Capniid genus. The trochantins of the pterothoracic segments encroach upon the katepisternum to an even greater extent than is the case in *Capnia*. The mesothoracic furcasternum, postfurcasternal plates, and spinasternum are closely united. The furcasternum is relatively large, has an arcuate anterior margin (sternacostal suture) and a straight or slightly arcuate and well defined posterior margin. Frequently a midventral suture partially splits the furcasternum. A similar suture along the mid-ventral line also often extends a short distance into the basisternum from the sternacostal suture. The spinasternum is long and narrow. The postfurcasternal plates are large and united with the spinasternum and furcasternum. The metathoracic furcasternum is similar in shape to that of the mesothorax but is slightly larger. It is not united with the first abdominal sternite.

WINGS.—The wing shape and venation of *Paracapnia* (Fig. 24) is similar to that of *Capnia* but differs in some very important details. R_1 of the fore wing is slightly curved cephalad at its base and then is bowed strongly caudad at a short distance beyond its point of origin. The first anal vein is straight. The second anal vein is very short and lies on the margin of the wing. The number of costal crossveins before the tip of the subcosta varies from none to three; beyond the subcosta there is only one costal crossvein or none at all in some cases. In the hind wing the first and second anal veins are long, straight, and about equal in length; the third anal vein has nearly disappeared. Cu_1 of the hind wing is practically always completely atrophied beyond m-cu. In a very few cases I have found conditions of partial atrophy of this apical portion of Cu_1 .

ABDOMEN.—The PREGENITAL SEGMENTS of the male abdomen are eight in number. Both the tergites and the sternites of all segments are completely sclerotized.

The pregenital sternites of the female are completely sclerotized. The first abdominal tergite is mostly membranous. The remaining pregenital segments are traversed by a mid-dorsal membranous stripe which is of one-third the width of the abdomen.

MALE TERMINALIA.—The ninth and tenth tergites are membranized mid-dorsally under the supraanal process. Two lateral portions of the tenth tergite are demarked. The recurved supraanal process is attached to the posterior mesal border of the tenth tergite (Fig. 53); it has no bulbous base. The ninth sternite (Fig. 41) bears no ventral appendage. The subgenital plate merges basally with the anterior region of the ninth sternite. It is demarked laterally from the rest of the ninth sternite by a distinct suture and a narrow region of membranization. Apically it bears a tiny nipple. The subanal lobes are roughly triangular in shape. Their mesal edges diverge posteriorly and are bluntly pointed apically. The fusion plate (Fig. 66) which lies between them is also bluntly pointed and gives to this combination of structures a trilobed apical margin. The fusion plate is parallel-sided and remarkably large. Anteriorly it is connected by membrane to a pair of comma-shaped retractoral plates. The

cerci are from 17 to 23 segmented and as long or longer than those of any other Capniid. Some of the subapical segments are as much as nine times as long as broad.

FEMALE TERMINALIA.—The membranous stripe that traverses the pregenital tergites also extends over segment eight and part of nine. The tenth tergite is completely sclerotized. The sternal plates, including the eighth sternite and the subanal lobes, are unmodified. The cerci are like those of the male.

Part III. Taxonomy of the Capniidae

Relative to other families of Plecoptera, the Capniidae are in good taxonomic order. It is a family composed of some seventy-five species distributed in twelve genera.

The genus *Capnia* was proposed by Pictet in 1841. Banks (1900) gave tribal rank to the genus on the basis of the absence of furcation of the radial sector beyond the cord in the fore wing. Klapalek (1905) raised the tribe to family rank on the basis of the following genitalic characters: (1) long cerci, (2) elongate supraanal process, (3) small subanal lobes. Banks (1906) discovered that the group may be characterized by the possession of only a single, unforked vein below the anal cell in the fore wing. Rostock, as early as 1892, was the first to note the sparsity of crossveins in the fore wing (in *Capnia* and *Capnopsis*). In their monograph of the Plecoptera (1925) Needham and Claassen used as family characters the many-segmented cerci, and the sparsity of crossveins in the fore wing; there is only one (or rarely two) mediocubital crossveins and one intercubital crossvein.

The abdominal characters (length of cerci, shape of supraanal process, size of subanal lobes) used by Klapalek to characterize the Capniidae are now known to be subject to too much variation to be of any significance. The number of cercal segments varies from many in several genera to only one in the genus *Capnioneura*. The supraanal process varies even in the single genus *Capnia* from a bulbous type to a much elongated type and from a unipartite to a bipartite condition; and the subanal lobes are not noticeably different in size from those of other families of stoneflies.

Two commonly used characters are very significant for distinguishing the Capniidae from other families: (1) the single unforked vein below the anal cell in the fore wing, and (2) the absence of a series of mediocubital and intercubital crossveins in the fore wing. The use of the single, unforked vein below the anal cell (Cu_2) in the fore wing as a family character breaks down in only one instance: in *Capnopsis* Cu_2 is absent. The importance of the presence of a single accessory crossvein between M and Cu_1 is constant for all known genera of Capniidae and has not been pointed out before. This vein is an even more constant feature in the Capniidae than the primary crossvein m-cu which is absent in *Capnopsis*. Almost invariably a single crossvein also occurs between Cu_1 and Cu_2 opposite the above mentioned crossvein.

A condition occurs in the male genitalia which is constant for all genera of Capniidae and which occurs in no other family of stoneflies. It is particularly

noteworthy since it has not been recognized previously as a family character. The subanal lobes of the males of all Capniidae are joined together mesally by an internally located plate which will be called the *fusion plate*. As early as 1896 Klapalek drew excellent figures of this structure in the male *Capnia nigra*. Since that time it has gone unnoticed by practically all Plecopterologists.

The Capniidae are considerably more closely related to the Leuctridae than to any other family (see especially the discussion under *Capnionera*). The parietal region of the head capsule is usually shorter in the Capniidae than in the Leuctridae, but intermediate conditions occur. The mouthparts of the two families are similar, but significant differences do occur, especially in the labium. The submentum of the Capniidae is hardly more than half as long as that of the Leuctridae, and the bases of the palpi are separated by a much narrower labiostipital region in the Capniidae than in the Leuctridae. On the basis of features of the labial palpi, head capsule, distance between furcal pits, shape of coxae, and male genitalia the Leuctridae are much more closely related to the Capniidae than to the Nemouridae under which family they are placed by some workers.

Generic Characters

Wing characters have been used extensively for generic distinctions in the Capniidae. Since wing venation offers excellent generic differences in this family a fairly good classification has resulted from their use. However, in the minds of some workers, there has been considerable doubt as to the validity of certain genera of Capniidae and even as to the family placement of some of them. Such misgivings are due to a still incomplete knowledge of the comparative morphology of numerous body structures. It is hoped that the findings of this present study will dispel some of this doubt.

I have been fortunate in having access to a large percentage of the known species and genera of Capniidae. Of most of them I have had genotypic material. Comparative studies of all external morphological details have been attempted in order to arrive at a basic understanding of generic relationships and characters. For the most part these studies confirm previous generic classifications, but in a few instances there are important contradictions.

I have found that the wings and thoracic sterna offer the best generic characters. The thoracic sterna exhibit a remarkable complexity of variations which are highly diagnostic. The diversity of shape and form that the mesothoracic furcasternum may assume in different genera of Capniidae is particularly noteworthy.* Several features of the thoracic pleural and dorsal regions of the labium and particularly of the male genitalia also exhibit significant generic differences. The legs, head capsule, mouthparts other than the labium, and the female genitalia seem to offer no generic characters.

In the citation of references in the following taxonomic discussions no attempt is made at completeness, since such a procedure would be merely a

* FRISON (1935) and UENO (1938) have already used the mesosternum of Capniidae for generic classification to a limited extent.

repetition of parts of the recently published Claassen catalogue. Only those papers which bear on the immediate subject are cited. In continually referring to the Capniid literature during this study a few errors existing in the literature in the synonymy of certain genera and species of Capniidae have come to my attention. These are corrected at appropriate points in the following pages.

CAPNIA Pictet, 1841

1841. *Capnia* Pictet, Perlides, pp. 318-320.

1897. *Arsapnia* Banks, Trans. Amer. Ent. Soc. **24**:22.

1900. *Capnura* Banks, Trans. Amer. Ent. Soc. **26**:241, 245. NEW SYNONYMY.

1906. *Arsapnia*, *Capnura*, Banks, Can. Ent. **38**:224.

1909. Enderlein, Zool. Anz. **34**:391 (*Capnia nigra* designated as genotype).

1924. Claassen, Can. Ent. **56**:43 (*Arsapnia* synonymized under *Capnia*).

1925. Needham & Claassen, Plecop. Amer. North of Mex., pp. 253-254.

1938. *Capnia* (*Arsapnia*), *Capnura*, Banks, Psyche **45**:73.

Containing nearly fifty described species *Capnia* is the largest genus in the Capniidae. Numerous species are known from the western United States and Canada, and a lesser number are distributed from the British Isles through Eurasia to Japan where four species occur. More than half of the known species are restricted to the North American continent.

The genus *Capnia* which was erected by Pictet in 1841 originally contained five species all except one of which have been removed to other genera of stoneflies. The single remaining species, *Capnia nigra* (Pictet) of Europe, was designated as genotype by Enderlein in 1909.

The species *Capnis opis* and another species described in this paper as new do not agree with *Capnia* in generic characters and therefore must be placed in a different genus (*Paracapnia* n.g.).

Capnia nigra, upon casual observation, appears to be generically different from other species of *Capnia* especially in male genitalic features. However, a study of a large percentage of the species in the genus shows, with but one exception, that features that have been accepted as generic or subgeneric characters within *Capnia* are merely extremes of highly variable structures. These extremes are bridged by numerous intermediate conditions except in the case of *Capnia nigra*. In this species the ninth sternite of the male bears a distinct median appendage of which there is no trace in any other species of *Capnia*. Although the presence or absence of a ventral lobe or appendage on the ninth sternite of the male has been used as a generic character in the Capniidae, it has not been so used in *Capnia*. This is fortunate because the presence of a ventral lobe in *Capnia nigra* is not supported by other constant characters that could be considered to be of generic or subgeneric value. Since *Capnia* is a large genus, apparently with active evolutionary tendencies, it is probable that conditions of the ninth sternite intermediate between that of *Capnia nigra* and those of other species of *Capnia* will be discovered as additional species are described. Even if such is not the case, one would hesitate to give generic or subgeneric rank to a single species on the basis of secondary sexual characters

that are distinctive of only one sex and are unsupported by other characters of generic or subgeneric value.

Although Claassen (1924) had not studied the genotype *Capnia nigra*, his synonymy of *Arsapnia* under *Capnia* is correct. When the genus *Arsapnia* was proposed in 1897 and keyed in 1907 by Banks, the length of the discal cell in proportion to the length of the region beyond the cord was used to distinguish the genus. This criterion cannot be used, however, because of the tremendous variations in the extent of brachypterism which affect particularly the distal region of the wing and thus greatly influence the proportionate sizes of the discal cell and region beyond the cord. In 1938 Banks removed *Arsapnia* from synonymy again and placed it as a subgenus of *Capnia* on the basis of the course of the first anal vein of the fore wing. In *Capnia nigra* he noted that the first anal vein is angularly bent near its base and has a conspicuous sclerotized patch within the angle. In *Arsapnia decepta* Banks found the first anal vein to be only gently curved and without a sclerotized patch. As has been discussed under the morphological treatment of *Capnia* in this article, numerous intermediate conditions between these two extremes occur within the genus *Capnia*. Wide variation may occur even within a single species. Therefore these characters are not available for generic or subgeneric distinctions.

The synonymy of the monotypic genus *Capnura* Banks under *Capnia* is also asserted here. A study of the type specimens of *Capnura venosa* Banks demonstrates no significant generic or subgeneric distinctions. The presence of crossveins beyond the cord (between R_1 and R_2) in the fore wing, the only perceivable differentiating character and the one which was used to define *Capnura* is highly variable. The number of crossveins varies even between the two fore wings of a single specimen. In the type specimens the number of such crossveins was found to vary from one to four. The highly variable condition of the number of crossveins in the apical region of the wing has recently been recognized to be more the rule than the exception in Plecoptera and must be considered in this case also to be of no value as a generic character. It is very likely that further collecting will disclose specimens in which apical crossveins are entirely lacking. The tendency toward the development of such crossveins is useful, however, as a secondary specific character.

It now becomes apparent because of variational tendencies within the genus *Capnia* that only the following few characters are distinctive of the genus. The sclerites of the mesosternum can be differentiated consistently from other genera of Capniidae. However, because of greater ease of use for taxonomic purposes, two wing characters that have been pointed out by Banks (1938) supply by far the best criteria for defining the genus: (1) R_1 of fore wing bent upward at its origin (Fig. 17); (2) first anal vein of fore wing bent abruptly caudad at its junction with cu-a and then curved outwardly again (Fig. 17).

CAPNIA FIBULA Claassen

This is a peculiar and interesting species which has been mentioned elsewhere in this paper because of the complete absence of wings which is accom-

panied by still other profound thoracic modifications. It deserves further mention here because of the inadequacy of previous descriptions.

Capnia fibula was described by Claassen (1924) from a single male and a female from New Mexico. Both type specimens are bleached nearly to transparency in alcohol. The female is fully winged. The type male is entirely wingless. In the original description of the species Claassen entered the wingspread as 12 mm?. In the Needham and Claassen monograph (1925) this figure was included without the question mark. Such a measurement is entirely misleading since the male has absolutely no wings at all (Fig. 39). A specimen of *Capnia fibula* at the Museum of Comparative Zoology is in far better condition than is the holotype at Cornell. I have included figures of the male genitalia (Figs. 57, 58) drawn from this specimen.

ALLOCAPNIA Claassen, 1924

1924. *Capnella* Claassen, Can. Ent. **56**:43-44 (*Capnella granulata* designated as genotype).
1928. *Allocapnia* Claassen, Ann. Ent. Soc. Amer. **21**:667 (new name for *Capnella* preoccupied by Gray in Coelenterata (1896)).
1929. *Capnella*, Ueno, Kontyu **4**:147-150.
1935. *Capnellula* Strand, Folia zool. et hydrobiol. **7**:304 (new name for *Capnella* preoc. by Gray).
1935. Frison, Ill. Nat. Hist. Survey Bull. **20**(4):355-356, fig. 287.
1938. Ueno, Kontyu **12**(5):168-172, figs. 7-16.

Genotype.—*Allocapnia granulata* (Claassen).

The genus *Allocapnia* was erected in 1924 to receive several North American species of Capniidae. Containing thirteen North American species and possibly some Japanese species it is now the second largest genus in the family.

Our North American species of *Allocapnia* form a very homogeneous group. Although I have not studied any of Ueno's four Japanese species, I am strongly led to suspect by his publications (1929, 1938) that perhaps all four of them belong in some other genus or genera, possibly new. If Ueno's (1938) sternal and wing venational drawings of his species *sikokuensis* are correct, this species certainly is not an *Allocapnia* but is very probably a *Capnia*. His species *bulba* almost certainly belongs in the genus *Eucapnopsis* (see discussion under *Eucapnopsis*). Ueno states that his species *tikumani* and *nivalis* are entirely wingless in both sexes. Therefore, these two species obviously cannot be placed generically on the basis of wing venation. However, Ueno's drawings of the thoracic sternum of *tikumani* and of the genitalia of both species are somewhat suggestive of *Allocapnia* and his assignment of these two species to this genus is possibly correct.

It has been suggested by Ueno that the genus *Takagriopteryx* Okamoto may be synonymous with *Allocapnia* (see discussion under *Takagriopteryx*). If this is found eventually to be true, the genus under discussion here must take the older name *Takagriopteryx*.

As has been mentioned in the morphological discussion, *Allocapnia* is

different from other Capniidae in numerous characters. Although almost any of these will serve to identify the genus, a complete listing of them is not desirable here. Any one of the following more easily observed characters will serve to identify *Allocapnia*: (1) Cu of hind wing unbranched (Fig. 18); (2) vannus of hind wing greatly developed, extending beyond cord (Fig. 18); (3) subcosta ending before cord (Fig. 18); (4) prothoracic spinasternum not fused at its lateral angles with the mesothoracic basisternum (Fig. 26); (5) anterior basalare immovably united with the posterior basalare except at its very tip (Fig. 35).

APTEROPERLA Matsumura, 1931

1931. *Apteroperla* Matsumura, 6000 illus. ins. Japan, p. 1426, fig. 15.

1938. Ueno, Kontyu 12:168.

Genotype.—*Apteroperla yazawai* Matsumura.

The original description is in Japanese and not understandable by me. Ueno (1938) has removed *Apteroperla* from Apteroperlidae, where it was originally placed, to the Capniidae. Matsumura's figure of the wingless female could easily be a Capniid and Ueno's judgment on this matter is probably correct. Ueno also suggests that *Apteroperla* may be synonymous with some other Capniid genus, probably *Allocapnia*.

CAPNIELLA Klapalek, 1920

1920. *Capniella* Klapalek, Acta Soc. Ent. Ceck. 17:5.

1936. *Neocapniella* Claassen, Ann. Ent. Soc. Amer. 29:622. NEW SYNONYMY.

Genotype.—*Capniella nodosa* Klapalek.

This genus, proposed in 1920 as *Capniella*, was given the new name *Neocapniella* by Claassen in 1936. Since the basis of this synonymy is *Capniella* Sahlberg, a nomen nudum (see discussion under *Capnopsis*), we must return to the original *Capniella* of Klapalek.

The genus and its type species (*C. nodosa* from Siberia) are based on two female specimens which we hope are still in existence somewhere in Europe. Klapalek made no figures, but the description seems well done and points out several peculiarities which seem to justify the erection of a new genus. He noted in the fore wing the fusion of Rs and M at their bases, a character unknown in other Capniid genera. Other peculiarities are the presence of two crossveins in the medial field beyond m-cu and a longitudinally keeled subgenital plate. The verification of these as generic characters must await an eventual more complete anatomical study.

CAPNIONEURA Ris, 1905

1905. *Capnioneura* Ris, Mitt. Schweiz. Ent. Ges. 11:93-95, figs. 1-2.

Genotype.—*Capnioneura nemuroides* Ris.

The genus *Capnioneura* was proposed by Ris in 1905 for the reception of

a single European species *nemuroides*. Two other species occurring in southern Europe are now known.

Ris found this genus to be distinct from all other Capniidae in that the cerci are reduced to a single segment. This condition of single-segmented cerci would usually be assumed to indicate closer affinity with the Nemouridae or the Leuctridae than with the Capniidae. However, Ris observed that the wing venation and genitalia are similar to those of *Capnia*. Thoracic and head characters also give overwhelming support to his conclusion as to its affinities.

For taxonomic purposes the genus can be characterized best by the following features: (1) a transverse suture extending across the frons immediately in front of the median ocellus (Fig. 4); (2) postfrontal sutures absent (Fig. 4); (3) both glossae and paraglossae demarked at their bases by sclerotic rims (Fig. 11); (4) mesothoracic furcasternum transverse and divided by a suture along the mid-ventral line (Fig. 27); (5) mesothoracic postfurcasternal plates united with the spinasternum, furcasternum, and sometimes with the furcasternal arms (Fig. 27); (6) male subgenital plate produced posteriorly under the subanal lobes (Fig. 46); (7) subanal lobes of male divided into two parts, extremely narrow (Fig. 46); (8) cerci one-segmented (Fig. 46); (9) wings with no costal crossveins (Fig. 19); (10) vannus of hind wing with four longitudinal veins (Fig. 19).

CAPNOPSIS Morton, 1896

1840. *Perla*, Zetterstedt, *Insecta Lapponica*, p. 1059.

1892. *Capnodes* Sahlberg, Berlin. Ent. Ztschr. 37:3, figs. 1-10.

1895. *Capniella* Sahlberg, Meddel. Soc. pro Fauna et Flora Fennica 21:107. NOMEN NUDUM.

1896. *Capnopsis* Morton, Trans. Ent. Soc. London 1896:61. (*Capnodes* preoccupied by Guenee 1852 in Lepidoptera).

1902. Kempny, Verh. k.k. Zool.-bot. Ges. Wien 52:227-229, fig. 1.

1940. *Capniella*, Claassen, Cornell Univ. Mem. 232:96-97.

Genotype.—*Capnodes schilleri* (Rostock (= *Capnopsis pygmaea* (Zett.))).

The genus *Capnopsis* contains only one species, but has nevertheless been the object of considerable synonymical confusion. In the recent Claassen catalogue this genus was placed under the name *Capniella* Sahlberg. *Capniella* is actually a *nomen nudum* since it was mentioned in a report as a bare name without definition or designation of any species to be included in it. Morton, in working over some Finnish material, informed Sahlberg of his progress. Sahlberg in reporting this information before a meeting of the Society pro Fauna et Flora Fennica mentioned the manuscript name *Capniella*. It may have been that Morton later discovered his manuscript genus *Capniella* to be the same as Rostock's genus *Capnodes* and thus never published it as a new genus.

The species *Capnopsis schilleri* (Rostock) was apparently justifiably synonymized under *C. pygmaea* (Zetterstedt) by Kempny in 1902, and Claassen's recognition of *C. schilleri* as a distinct species in his catalogue must be considered incorrect. His synonymy of *Capnia tenuis* under *Capnopsis pygmaea* is

also obviously incorrect since *C. tenuis* is a true *Capnia* and therefore could not possibly be synonymous with a species of *Capnopsis*.

Capnopsis is a most remarkable genus of Capniidae. It may be characterized by the following combination of characters: (1) coronal and postfrontal sutures of head absent; (2) paraglossae delimited basally by a sclerotic rim (Fig. 12); (3) labial palpi, when extended forward, project beyond the glossae and paraglossae; (4) metathorax relatively small; (5) 1st A of fore wing short and straight; 2nd A absent (Fig. 20); (6) in hind wing, a vannus and vannal veins are absent; only the anal cell remains (Fig. 20); (7) m-cu absent in both fore and hind wings (Fig. 20).

EUCAPNOPSIS Okamoto, 1922

1922. *Eucapnopsis* Okamoto, Bull. Agri. Exp. Sta. Chosen 1(1):8 (*E. stigmatica* n. sp. designated as genotype).
1924. *Capnia*, Claassen, Can. Ent. 56:55-56 (*C. brevicauda* n. sp.).
1925. *Capnia*, Needham & Claassen, Plecop. Amer. North of Mex., p. 269.
1929. *Capnia*, Ueno, Mem. Coll. Sci., Kyoto Imp. Univ., Ser. B, 4:141.
1934. Neave, Can. Ent. 66:5-6.
1935. Frison, Ill. Nat. Hist. Survey Bull. 20(4):352, 354.
1937. Frison, Ill. Nat. Hist. Survey Bull. 21(3):86.
1942. Frison, Ill. Nat. Hist. Survey Bull. 22(2):237, 238.

Genotype.—*Eucapnopsis stigmatica* Okamoto.

The genus *Eucapnopsis* was proposed as a genus of Capniidae by Okamoto in 1922 for two Japanese species. A North American species, *brevicauda*, has also been placed in this genus.

Okamoto based the genus principally on the two following characters: (1) cerci composed of very few segments; (2) ninth sternite of male with a basal median lobe. Needham and Claassen and Ueno have subsequently failed to recognize *Eucapnopsis* as distinct from the genus *Capnia*. Frison, however, has recognized it as distinct and, until recently (1942) has even placed it in a different family (Leuctridae). A morphological study of *Eucapnopsis* leaves no doubt that it is a valid genus and that it belongs in the Capniidae and not in the Leuctridae. In returning *Eucapnopsis* to the Capniidae Frison (1942 p. 238) used the number of cercal segments as the primary family character and found it necessary to key *Eucapnopsis* out at a point different from that of the remaining genera of Capniidae. It is obvious, however, that in a family where the number of cercal segments varies from one to twenty-five or thirty, such a character can be of virtually no use as a family criterion. The primary family characters are to be found in the sparsity of supplementary crossveins in the fore wing, in the unbranched condition of the second anal vein of the fore wing, in features of the mouthparts particularly of the labium, and in the fusion plate of the subanal lobes of the male. All known genera of Capniidae conform exactly with this combination of characters with but one minor exception. The highly specialized genus *Capnopsis* has lost the second anal vein of the fore wing.

Ueno's species *Allocapnia bulba* will eventually be transferred to the genus

Eucapnopsis, I believe. On the basis of wing venation and male genitalia it does not conform to the genus *Allocapnia* in which Ueno has placed it. However, the genitalia of *bulba* (Ueno 1929, fig. 25C) are so similar to those of our species *E. brevicauda* as to appear almost conspecific with it. Its cerci are of the abbreviated *Eucapnopsis* type and the wings (Ueno 1929, fig. 25A) except for slight apical brachyptery are similar to those of our species of *Eucapnopsis*. Ueno does not mention the presence of a lobe on the ninth sternite of the male but he might easily have overlooked such a structure.

Eucapnopsis is characterized by the following features: (1) R_1 of fore wing not bowed at base (Fig. 21); (2) first anal vein of fore wing straight (Fig. 21); (3) mesothoracic furcasternum small, narrowly transverse (Fig. 28); (4) mesothoracic postfurcasternal plates entirely surrounded by membrane (Fig. 28); (5) presternal sclerites of all three thoracic segments free from the basisternum (Fig. 28); (6) cerci four to five segmented (Fig. 47); (7) ninth sternite of male with a ventral appendage (Fig. 47). Some of the characters listed above also occur in other genera but the entire combination never occurs in any other genus. For example, on wing venation it is not possible to separate *Nemocapnia* from *Eucapnopsis* with absolute certainty, but the thoracic sternal patterns of the two genera are entirely distinct as are also the ninth sternites of males of the two genera.

ISOCAPNIA Banks, 1938

1938. *Isocapnia* Banks, *Psyche* 45:73-74 (*Arsapnia grandis* Banks designated as genotype).

1942. Frison, *Pan-Pacific Ent.* 18:68-69.

Genotype.—*Arsapnia grandis* Banks.

The genus *Isocapnia* was erected by Banks in 1938 with the North American species *Arsapnia grandis* Banks designated as genotype. Three or four North American species in this genus are known. Banks characterized the species of *Isocapnia* as follows: R at origin of R_s straight; anal area of hind wing reaching not more than three-fourths of the way to wing tip; one oblique crossvein beyond end of subcosta; setae very long; usually five or six costal crossveins; large species. To this Frison (1942) added: females with very narrow, median, longitudinal, membranous stripe extending across abdominal tergites one through eight; and males with a lobe at the base of the ninth abdominal sternite. Most of the above characters appear to be valid generic distinctions. In addition, several previously unrecognized, and in some cases more basic characters, might be mentioned. I consider the following features to be of significance as generic characters: (1) R_1 and 1st A of fore wing straight at base (Fig. 22); (2) paraglossae partially demarked from the labiostipites (Fig. 14); (3) postalar bridge present on both pterothoracic segments; (4) mesepimeron with a transverse dark band; (5) mesothoracic furcasternum poorly demarked from the postfurcasternal plates with which it is united (Fig. 29); (6) metathoracic furcasternum united with and poorly demarked from the first abdominal sternite (Fig. 29); (7) prothoracic presternum broadly

fused with the basisternum (Fig. 29); (8) basal region of ninth abdominal sternite separate from the subgenital plate and bearing a broadly rounded median, ventral appendage (Fig. 50); (9) female with a narrow, median, longitudinal, membranous stripe extending across abdominal tergites two through eight.

NAPCIA Navas, 1917

1917. *Napcia* Navas, R. Acad. Cien. y Artes Barcelona, Mem. 13(26):8(398).

Genotype.—*Capnia libera* Navas.

I know nothing of this genus since only a single paper concerning it has been written and this has not been accessible.

NEMOCAPNIA Banks, 1938

1938. *Nemocapnia* Banks, Psyche 45:73, 74.

1942. Frison, Ill. Nat. Hist. Survey Bull. 22(2):262-264.

Genotype.—*Nemocapnia carolina* Banks.

The genus *Nemocapnia* was proposed by Banks (1938) for a single new North American species *carolina*. Banks defined the genus as follows: R straight at origin of Rs; anal area of hind wing reaching not more than three-fourths of the way to wing tip; no crossvein beyond end of subcosta; cerci short (7-8-segments); slender species. Of the characters mentioned above only the number of cercal segments will distinguish the genus from closely related genera.

Nemocapnia can be recognized easily by the following combination of characters: (1) presterna of all thoracic segments merge with the basisternum of the segment concerned (Fig. 30); (2) mesothoracic furcasternum narrowly transverse and not divided by a suture along the mid-ventral line (Fig. 30); (3) meso-thoracic spinasternum extremely narrow (Fig. 30); (4) mesothoracic postfurcasternal plates large and united to the spinasternum and furcasternum (Fig. 30); (5) meso- and metathoracic epimeron partially divided into anepimeron and katepimeron by a groove; (6) in fore wing, R_1 straight at base, 1st A slightly curved just beyond cu-a (Fig. 23); (7) no costal crossvein beyond Sc (Fig. 23); (8) cerci 6 to 7-segmented; (9) subgenital plate of male distinctly demarked but not separated along lateral margins from remainder of 9th sternite by membrane (Fig. 51).

PARACAPNIA gen. nov.

Genotype.—*Paracapnia curvata* n. sp.

This new genus contains two species of Eastern North American Capniidae. One of its species *P. opis* (Newman) has until this time been assigned to *Capnia*. Such an assignment is definitely incorrect, however, since numerous features of practically all parts of the body distinguish it from *Capnia* and from all other Capniidae. I have designated *P. curvata* as genotype since the identity of *P. opis* is not yet definitely settled.

For taxonomic purposes the genus can be characterized best by the following features: (1) postfrontal and coronal sutures absent; (2) paraglossae usually narrower than the glossae (Fig. 16); (3) furcasternum of meso- and metathorax transverse and nearly rectangular (Fig. 40); (4) mesothoracic post-furcasternal plates large and united with the furcasternum and the spinasternum (Fig. 40); (5) R_1 of fore wing bent caudally shortly beyond its base; 1st A straight (Fig. 24); (6) apical portion of Cu_1 of hind wing atrophied (Fig. 24); (7) subgenital plate of male separated laterally from the rest of the 9th sternite by a narrow band of membrane (Fig. 41); (8) fusion plate of subanal lobes of male parallel-sided or nearly so and unusually large; with a pair of retractoral plates (Fig. 66).

KEY TO SPECIES OF PARACAPNIA

Supraanal process of male angulate at base, projecting forward and tapering toward apex, 0.40 to 0.50 mm. long *P. opis*
Supraanal process of male not angulate at base, thinner than that of the above species, projecting forward and tapering slightly toward apex, 0.55 to 0.60 mm. long *P. curvata*

Paracapnia curvata n. sp.

Fig. 53

As has been pointed out previously (Hanson 1943) the identity of *Paracapnia opis* is not yet definitely established but must for the present be accepted as defined by Ricker (1938) who studied the genitalia of the type.

Several specimens of *Paracapnia* that I have in my collection differ consistently from numerous specimens of *P. opis* that I have studied from several widely separated localities. The females of the two species seem to be indistinguishable but the males can be distinguished easily by the shape and length of the supraanal process (see key).

This species conforms in all general morphological details with the description of *Paracapnia* given in the preceding pages. Length to tip of wings, 6 to 7 mm. in the male, 6 to 9 mm. in female; length of body, 4 to 5 mm. in male, 6 to 8 mm. in female; length of fore wing, 4 to 5 mm. in male, 6 to 7 mm. in female.

Male.—Abdominal tergites without protuberances or other sclerotic modifications. Ninth tergite with a narrow median sagittal band of membrane. Supraanal process recurved, not angulate at base, projecting forward and tapering slightly toward the apex; 0.55 to 0.60 mm. long. The dorsal region of the supraanal process is largely membranous, especially toward the apex. This membranous portion may bulge upward so as to open the genital tube within the supraanal process. When in this condition the supraanal process does not appear to taper toward the apex in lateral view but may even expand apically.

Female.—Posterior margin of eighth abdominal sternite broadly rounded. A broad median region is indistinctly demarked; it bears a small, mesal light colored or membranous spot on the posterior margin. The ninth sternite is

unmodified except for a transverse region of membranization along the posterior border of the segment.

Collection Data.—*Holotype* male, *allotype* female—Arietta, Hamilton Co., N. Y., alt. 1800 ft., April 5, 1937 (Alexander). *Paratopotypes*—1 ♂ 1 ♀. *Paratypes*—Sacandaga River, Wells, N. Y., April 3, 1937 (Alexander) 2 ♂ 3 ♀. Cook Co., Minn., April 25, 1940 (Harden) 3 ♂: April 28, 1940 (Harden) 1 ♀. A male paratype from Minnesota has been deposited in the Museum of Comparative Zoology at Cambridge and one in the Collection of the Illinois State Natural History Survey at Urbana. The remaining type specimens are in my personal collection.

TAKAGRIPTERYX Okamoto, 1922

1922. *Takagripteryx* Okamoto, Bull. Agr. Exp. Sta. Gov.-Gen. Chosen 1:3.
1929. Ueno, Mem. Coll. Sci., Kyoto Imp. Univ., Ser. B, 4:150.

Genotype.—*Takagripteryx nigra* Okamoto.

The genus *Takagripteryx* was proposed in 1922 by Okamoto for a single Japanese species *T. nigra* Okamoto which he placed in the family Leptoperliidae. Claassen (1924) has transferred the genus to the Capniidae where it obviously belongs. Ueno (1929) has suggested that the genus may be synonymous with *Allocapnia*. However, Okamoto figures the cubitus of the hind wing as being branched while the cubitus of the hind wing of all North American species of *Allocapnia* is unbranched. The atrophy of the apical portion of Cu₁ of the hind wing may also be a significant difference. In addition, Okamoto describes *Takagripteryx* as having an unipartite supraanal process while all other known species of *Allocapnia* have a bipartite supraanal process. Therefore, I am inclined to believe that *Takagripteryx* is a valid genus.

No specimens of this genus have been available for study.

List of the Species of Capniidae of the World

ALLOCAPNIA Claassen

curiosa Frison
**forbesi* Frison
**granulata* (Claassen)
**illinoensis* Frison
**maria* Hanson
**minima* (Newport)
**mystica* Frison
**nivalis* (Ueno)
**pygmaea* (Burmeister)
**recta* (Claassen)
**richeri* Frison
**sikokuensis* Ueno
**tikumani* Ueno
**virginiana* Frison
**vivipara* (Claassen)

APTEROPERLA Matsumura

yazawai Matsumura

CAPNIA Pictet

affinis Morton
apicalis Navas
**atra* Morton
**bakeri* (Banks)
barbata Frison
**barberi* Claassen
bituberculata Ueno
**californica* Claassen
**coloradensis* Claassen
**columbiana* Claassen
**confusa* Claassen
conica Klapalek

* Species marked with an asterisk have been studied during the preparation of this paper.

CAPNIA (Continued)

**decepta* (Banks)
 **distincta* Frison
dusmeti Navas
elevata Frison
 **elongata* Claassen
 **excavata* Claassen
 **fibula* Claassen
 **glabra* Claassen
 **gracilaria* Claassen
 **hantzchi* Ricker
japonica Okamoto
jewetti Frison
limata Frison
 **manitoba* Claassen
maynari Navas
melia Frison
 **nana* Claassen
 **nearctica* Banks
 **nigra* (Pictet)
 **oenone* Neave
oklandi Morton
oregona Frison
praerupta Bengtsson
 **projecta* Frison
 **promota* Frison
sparre schneideri
 Esben-Petersen
 **spinulosa* Claassen
storkani Samal
takahashii Okamoto
 **teresa* Claassen
 **tumida* Claassen
umpqua Frison
variabilis Klapalek
 **venosa* (Banks)
vidua Klapalek
wanica Frison
zaicevi Klapalek

CAPNIELLA Klapalek

nodosa Klapalek

CAPNIONEURA Ris

brachyptera Despax
mitis Despax
 **nemuroides* Ris

CAPNOPSIS Morton

**pygmaca* (Zetterstedt)

EUCAPNOPSIS Okamoto

**brevicauda* (Claassen)
bulba (Ueno)
stigmatica (Okamoto)
4-segmentata (Okamoto)

ISOCAPNIA Banks

abbreviata Frison
 **crinita* (Needham & Claassen)
 **grandis* (Banks)
 **integra* Hanson

NAPCIA Navas

libera (Navas)

NEMOCAPNIA Banks

**carolina* Banks

PARACAPNIA Hanson

**curvata* Hanson
 **opis* (Newman)

TAKAGRIPOPTERYX Okamoto

nigra Okamoto

ABBREVIATIONS

1—first axillary sclerite
 2—second axillary sclerite
 3—third axillary sclerite
 A—anal vein
 a—anal crossvein
 ab—anterior basalar
 aepm—anepimeron
 aes—anepisternum
 af—antennifer
 al—alifer
 anp—anterior notal wing process
 ar—arolium
 arc—arculus
 as—antennal suture
 asc—antennal sclerite
 ata—anterior tentorial arm

bc—basicardo
 bg—basigalea
 bp—basipulvillus
 bpl—basal plate
 bs—basisternum
 C—costa
 ce—cercus
 cep—cephalinger
 cl—clypeus
 co—condyle
 ct—corporotentorium
 Cu—cubitus
 cu—cubital crossvein
 cu-a—cubito-anal crossvein
 cx—coxa
 dc—disticardo

ABBREVIATIONS—Continued

dg—distigalea	pls—pleural suture
dta—dorsal tentorial arm	pm—pleurostoma
epi—epiproct	pms—pleurostomal suture
epm—epimeron	pn—pronotum
eps—episternum	pnp—posterior notal wing process
es—epistomal suture	po—postcoxal bridge
esr—epistomal ridge	poa—postalar bridge
etn—eutrochantin	poc—postocciput
eye—compound eye	pocs—postoccipital suture
fe—femur	pr—precoxal bridge
fp—fusion plate	pra—prealar bridge
fr—frons	prs—presternum
fs—furcasternum	ps—parastipes
fsp—furcal pit	psc—prescutum
fsa—furcasternal arm	pscl—postscutellum
ge—gena	pla—posterior tentorial arm
gl—glossa	plar—pretarsus
h—humeral crossvein	R—radius
hm—hypostoma	r—radial crossvein
hms—hypostomal suture	r-m—radiomedial crossvein
hp—humeral plate	rp—retractoral plate
kepm—katepimeron	Rs—radial sector
kes—katepisternum	s—scape
la—lacinia	sa—supraanal process
lbi—labiostipites	sbl—subanal lobe
lc—lateral cervical sclerite	sbp—subgenital plate
lp—labial palpus	Sc—subcosta
lr—labrum	scl—scutellum
M—media	sct—scutum
m-cu—mediocubital crossvein	si—stipes
md—mandible	sm—submentum
me—meron	sp—spiracle
mh—mouth	sps—spiracular sclerite
mn—mentum	ss—spinasternum
mo—mola	sub—subalar sclerite
mxxp—maxillary palpus	sus—suspensoria
oc—ocellus	st—abdominal sternite
occ—occipital condyle	stc—sternacostal suture
or—orbicula	t—abdominal tergite
os—ocular suture	ta—tarsus
osc—ocular sclerite	tc—tentorial callosity
p—pedicel	tg—tegula
par—parietal sclerite	ti—tibia
pb—posterior basalare	tn—trochantin
pc—precosta	tr—trochanter
pfs—postfrontal suture (one arm of epicranial suture)	un—ungue
pge—postgena	ut—unguitractor
pgl—paraglossa	va—ventral appendage or lobe
	vc—ventral cervical sclerite

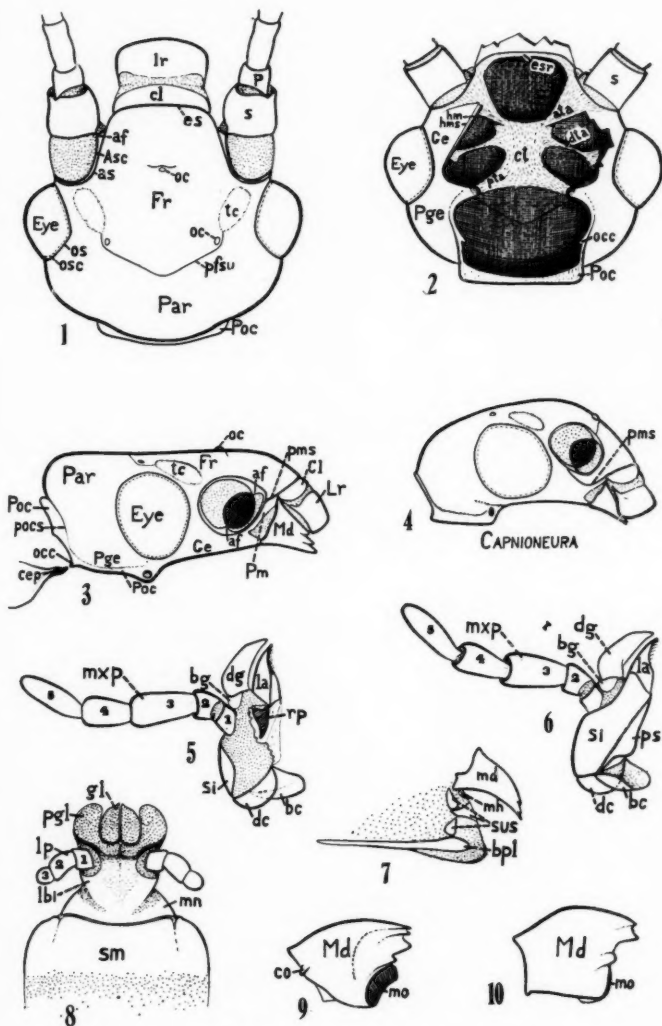


PLATE 1.—Figures 1-3, 5-10. *Capnia nigra*. 1. Head capsule, dorsal view. 2. Head capsule and tentorium, ventral view. 3. Head capsule, lateral view. 4. Head capsule of *Capnioneuria*, lateral view. 5. Left maxilla, dorsal view. 6. Right maxilla, ventral view. 7. Hypopharynx, lateral view. 8. Labium. 9. Left mandible, ventral view. 10. Right mandible, dorsal view.

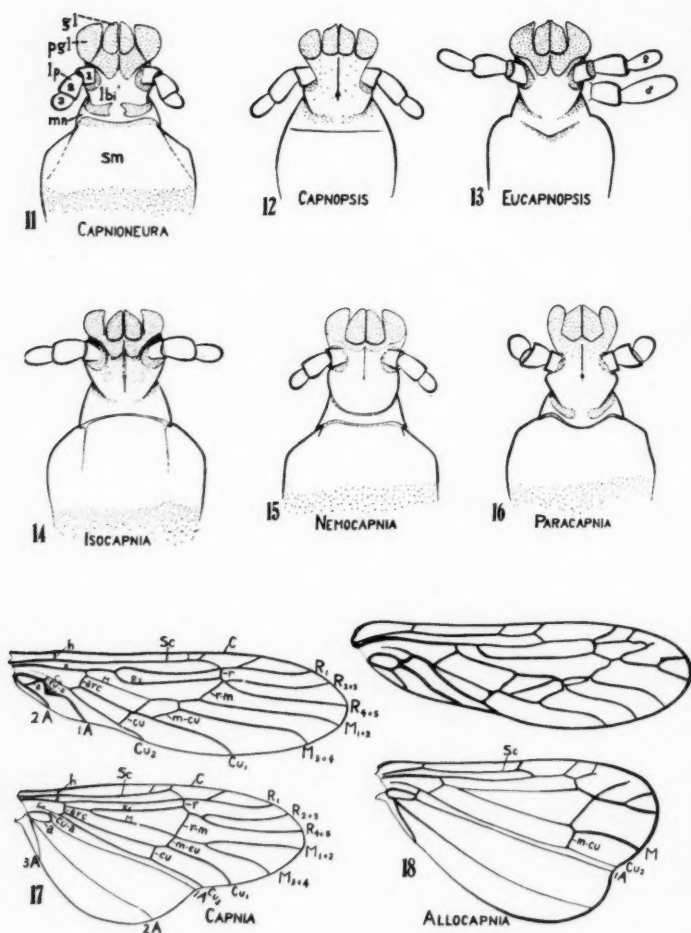


PLATE 2.—Figure 11. *Capnionura*, labium. 12. *Capnopsis*, labium. 13. *Eucapnopsis*, labium. 14. *Isocapnia*, labium. 15. *Nemocapnia*, labium. 16. *Paracapnia*, labium. 17. *Capnia nigra*, wings. 18. *Allocapnia*, wings.

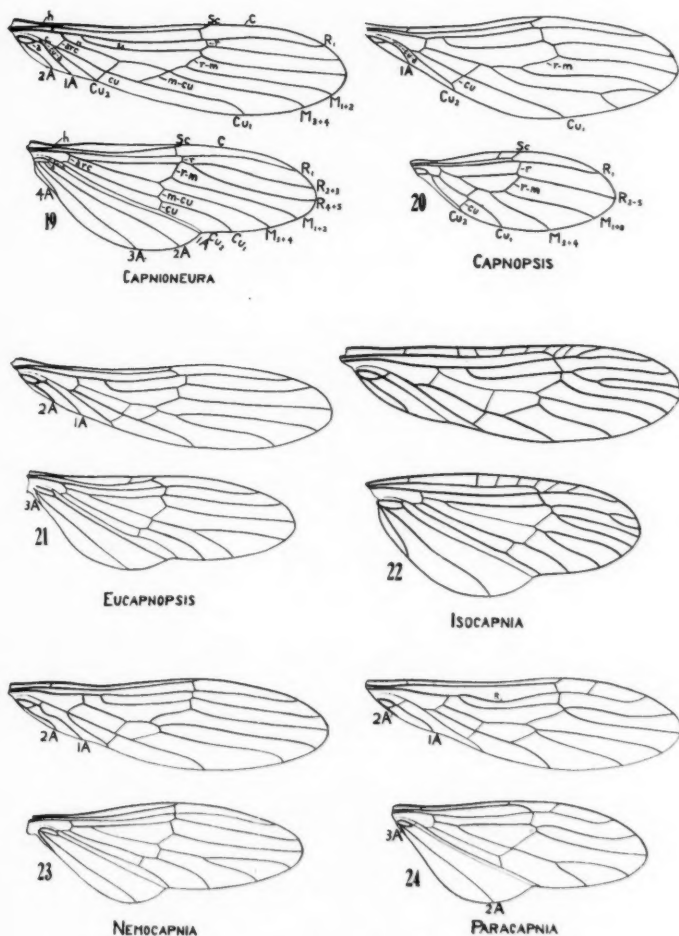


PLATE 3.—Figure 19. *Capnionneura*, wings. 20. *Capnopsis*, wings. 21. *Eucapnopsis*, wings. 22. *Isocapnia*, wings. 23. *Nemocapnia*, wings. 24. *Paracapnia*, wings.

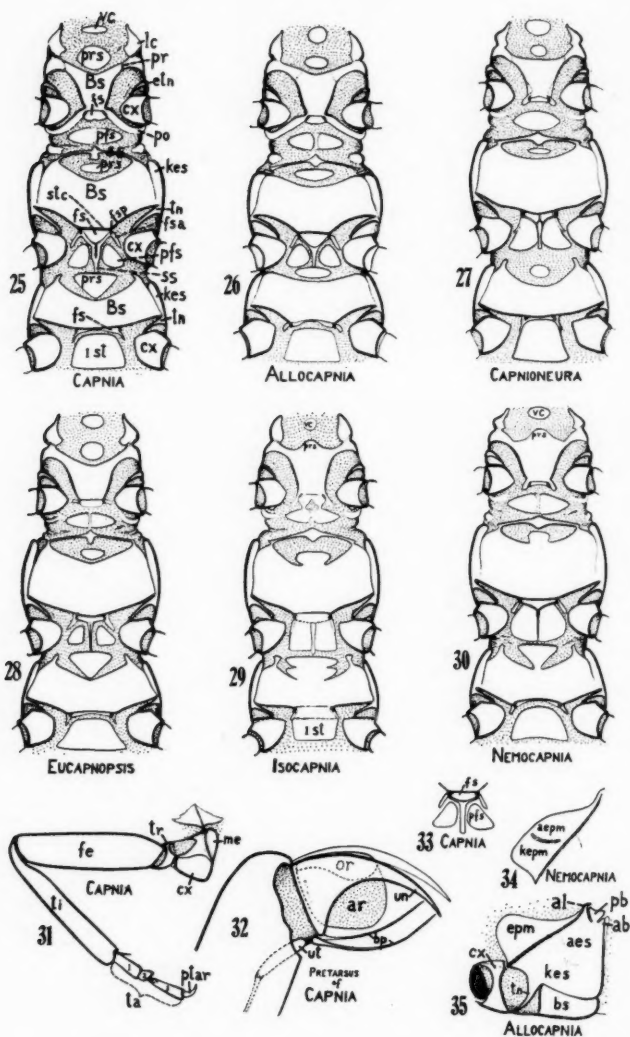


PLATE 4.—Figure 25. *Capnia nigra*, thoracic sternum. 26. *Allocapnia*, thoracic sternum. 27. *Capnioneura*, thoracic sternum. 28. *Eucapnopsis*, thoracic sternum. 29. *Isocapnia*, thoracic sternum. 30. *Nemocapnia*, thoracic sternum. 31. Middle leg of *Capnia*. 32. Pretarsus of *Capnia*. 33. Furcasternum of *Capnia* sp. 34. Epimeron of *Nemocapnia*. 35. Mesopleuron of *Allocapnia*.

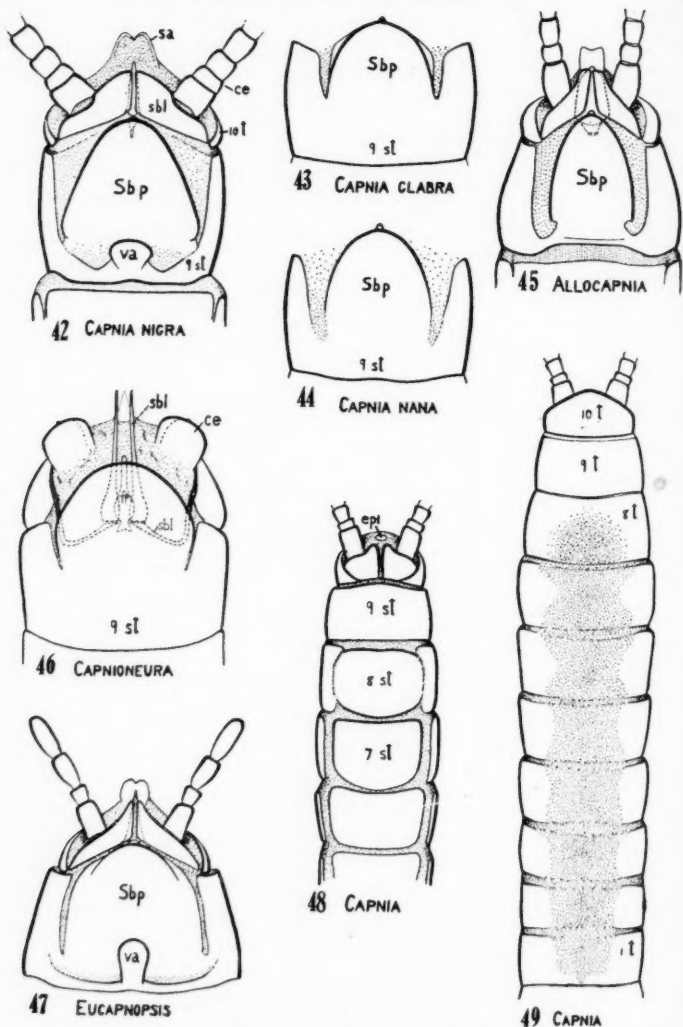
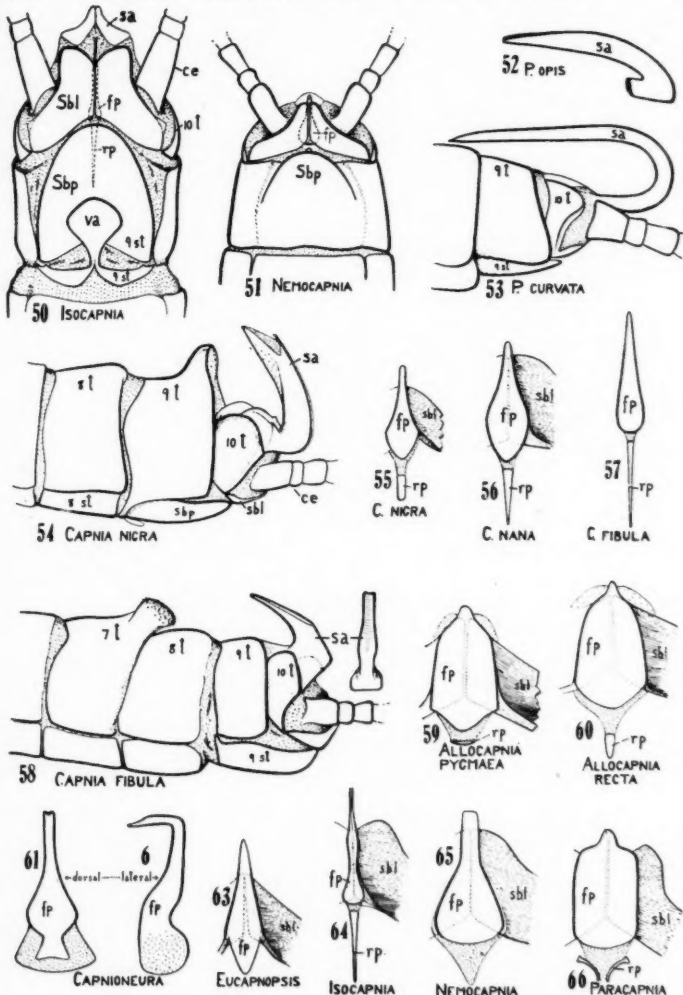


PLATE 6.—Figure 42. *Capnia nigra*, male genitalia, ventral view. 43. *Capnia glabra*, ninth sternite of male. 44. *Capnia nana*, ninth sternite of male. 45. *Allocapnia*, male genitalia, ventral view. 46. *Capnioneura*, male genitalia, ventral view. 47. *Eucapnopsis*, male genitalia, ventral view. 48. *Capnia nigra*, abdomen of female, ventral view. 49. *Capnia nigra*, abdomen of female, dorsal view.

PLATE 7.—Figure 50. *Isocapnia*, male genitalia, ventral view. 51. *Nemocapnia*, male genitalia, ventral view. 52. *Paracapnia opis*, supraanal process.



lateral view. 53. *Pacapnia curvata*, male genitalia, lateral view. 54. *Capnia nigra*, male genitalia, lateral view. 55. *Capnia nigra*, fusion plate, internal view. 56. *Capnia nana*, fusion plate, internal view. 57. *Capnia fbulu*, fusion plate, internal view. 58. *Capnia fbulu*, male genitalia, lateral view. 59. *Allocapnia pygmaea*, fusion plate, internal view. 60. *Allocapnia recta*, fusion plate, internal view. 61. *Capnioneura*, fusion plate, internal view. 62. *Capnioneura*, fusion plate, lateral view. 63. *Eucapniopsis*, fusion plate, internal view. 64. *Isocapnia*, fusion plate, internal view. 65. *Nemocapnia*, fusion plate, internal view. 66. *Paracapnia*, fusion plate, internal view.

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Studies on North American Water Snakes—II The Subspecies of *Natrix valida*

Roger Conant

The water snakes of western Mexico have long been the subjects of much confusion and very little interest. Following the first descriptions and the assignation of names to several pattern variations, they have remained conspicuously absent from herpetological literature except for their inclusion in the many faunal lists of the regions in which they occur.

Despite the fact that these snakes obviously are common in many parts of their range, only one hundred twenty-eight specimens are preserved in American museums, and of these but thirty-one are from the mainland of Mexico; the others are from the southern tip of the Mexican Territory of Baja California. Sizable series are available from few localities. Despite the comparative paucity of material it seems advisable to summarize the present status of our knowledge of *Natrix valida* (Kennicott) and its peninsular subspecies and to point out several problems that need to be studied. Interest in Mexican herpetology has grown remarkably in recent years, and, thanks to the several collectors who have encountered this species in the field, it is possible to assemble some information on habits and habitats. All the museum specimens have been studied, but I have seen neither *valida* nor *celaeno* in life.

Natrix valida and what have been considered as two of its principal synonyms all were described in 1860 in the Proceedings of the Academy of Natural Sciences of Philadelphia. Kennicott (p. 334) based *valida* on a specimen from Durango and placed it in the genus *Regina*. Cope (p. 341) described *Tropidonotus celaeno* and *T. tephropleura* from one and two specimens, respectively, from Cabo San Lucas, Baja California.

On the basis of pattern all apparently were different species—the type of *valida* was “uniform light brownish ash . . . with about every alternate scale on the fourth and fifth rows marked with black on each side near its base”; the type of *celaeno* was almost uniform black except for a lateral stripe of “lead gray . . . occupying the second, third, and part of the first row of scales”; and the types of *tephropleura* were spotted, at least when the skin was stretched. Cope, in his description of *tephropleura*, stated that the head differed in shape from the head of *valida*. Later (1861, p. 298) he called attention to the marked similarity of the two forms and placed *tephropleura* in the synonymy of *valida*. It is now known that there is considerable sexual and ontogenetic variation in the shapes and sizes of the heads of water snakes and that this characteristic is of little diagnostic value. In scutellation all three of the supposed species were very similar.

From the material now at hand it is possible to make the following observations: (1) All the specimens from mainland Mexico (coastal regions from

central Sinaloa to central Guerrero) are referable to Kennicott's *valida*. (2) Specimens from the Cape Region of Baja California show a tremendous amount of variation in pattern. A majority agree with Cope's *celaeno* whereas others are indistinguishable from mainland *valida*. Several are much more heavily spotted than in typical *valida*; in such specimens the dark markings, which are relatively small and inconspicuous in most *valida*, are basically similar, but they are larger or much more numerous, or both.

On the basis of pattern, ninety-five specimens from Baja California may be sorted roughly into four groups (see figure 1):

- (A) Snakes similar to mainland *valida* (light colored but indistinctly marked with small dark spots)—13 specimens.
- (B) Light colored snakes conspicuously marked with dark spots—17 specimens.
- (C) Dark snakes with black heads; dorsal surfaces with indistinct indications of pattern; a light lateral stripe on each side of the body—23 specimens.
- (D) Dark snakes, uniform black or dark brown above and below, except for a light lateral stripe on each side of the body—42 specimens.

There is almost complete intergradation of pattern between Groups A and B and probably no two persons would agree exactly in assigning specimens to the one or the other. The same situation exists in regard to Groups C and D, especially in view of the fact that fading of dark individuals (from long preservation) has a tendency to bring out evidences of pattern. Snakes which, in life, probably belonged to Group D are now classifiable in Group C. Specimens of both Groups C and D check with Cope's description of *celaeno* and may be considered as typical of that form.

Between Groups B and C, however, there is a hiatus which may be more apparent than real. Several older specimens, now very much faded, have been assigned to Group B, although it is possible that in life they may have been intermediate. At least two individuals definitely are so: (a) USNM 37545, in which the head is dark (probably black originally), the dorsum uniform brown, and the lateral stripe only very faintly defined; and (b) USNM 12642e, with a dark head, which would place it in Group C or D, and a conspicuously spotted body, which would classify it as a member of Group B. The original description of *tephropleura* indicates that Cope's specimens of this form also may have been somewhat intermediate between Groups B and C. It is impossible to check, however, for the types apparently are no longer in existence. The snakes catalogued in the National Museum (4683a-f) as the types of *tephropleura*, agree neither in pattern nor in details of scutellation with Cope's description.

It is possible that additional collecting may yield other more or less intermediate individuals. Such specimens would further help to bridge the gap between Groups B and C and validate the inference that there is complete intergradation in the Cape Region from specimens indistinguishable from mainland *valida* to those that are melanistic (except for the lateral stripe on each side).

In scutellation all the specimens from Baja California are in close agreement with one another.

From the above it is obvious that the water snakes of Baja California represent a mixed population in which numerous genetic factors find expression in

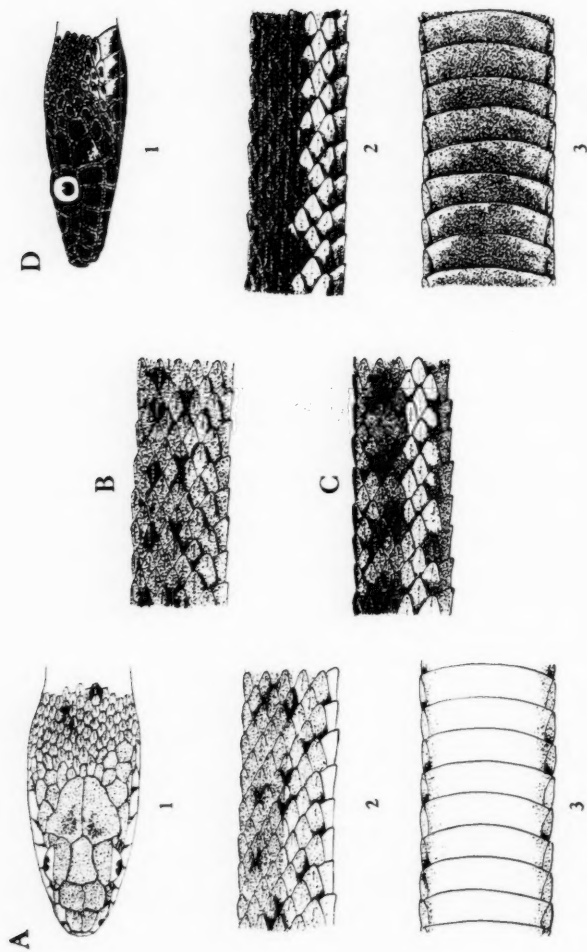


Fig. 1. Patterns and scutellation in *Natrix valida valida* and *Natrix valida celacno*. A (1, 2, & 3)—*valida* from Mazatlán, Sinaloa (EHT-HMS 4604 ♂). Some specimens of *celacno* (designated in the text as Pattern Type A) are similarly marked. B (Pattern Type B)—*celacno* from Santiago, Baja California (CAS 45943 ♀). C (Pattern Type C)—*celacno* from Agua Caliente, Baja California (CAS 45932 ♀). D (1, 2, & 3) (Pattern Type D)—*celacno* from Agua Caliente, Baja California (CAS 45894 ♂). Drawings by Doris M. Cochran.

a wide variety of patterns. Inasmuch as the majority of specimens agree with *celaeno*, as diagnosed by Cope, the name *celaeno* may be applied to the peninsular population as a whole.

The relationship between the mainland population of *Natrix valida* and that of the Cape Region of Baja California parallels one of the theoretical cases outlined by Dunn (1934) in his "Systematic Procedure in Herpetology." One type of geographic intergradation (according to him) exists when "one island has both strains (of a population) with one in a clear majority and the other island has only the other strain." In the present case the Cape Region and mainland Mexico may be considered as "islands" effectually separated by the Gulf of California.

The situation also nearly parallels Dunn's hypothetical case 2b in a later paper (1943, p. 127). In this he indicates that the two races of a species may differ in essential characteristics, although the population occurring in one region may include a small percentage of individuals which are indistinguishable from those of the other region.

In view of the above, *valida* and *celaeno* are here considered as being geographic races of the same species.

NATRIX VALIDA VALIDA (Kennicott)

Synonymy

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1887. *Regina valida valida* COPE, *Id.*, p. 74.
1892. *Natrix valida valida* COPE, Proc. U. S. Nat. Mus., vol. XIV [1891], p. 670. —COPE, Rep. U. S. Nat. Mus., 1900 [1898], p. 984, fig. 259.
1896. *Natrix valida* DUGÉS, Naturaleza, 2nd Ser., vol. II, pp. 481, 484-5. —VAN DENBURGH, Proc. Acad. Nat. Sci. Philadelphia, vol. XLIX, 1898 [1897], p. 464. —STEJNEGER and BARBOUR, Check List N. Amer. Amph. & Rept., ed. 1, 1917, p. 97. —SCHMIDT, Bull. Amer. Mus. Nat. Hist., vol. XLVI, 1922, p. 693. —VAN DENBURGH, Rept. Western N. Amer., California Acad. Sci., 1922, p. 784. —STEJNEGER and BARBOUR, *Supra*, ed. 2, 1923, p. 109. —BLANCHARD, Pap. Michigan Acad. Sci. Arts Lett., vol. IV, 1925, p. 12. —STEJNEGER and BARBOUR, *Supra*, ed. 3, 1933, p. 118.

—DITMARS, Rept. N. Amer., 1936, p. 161, pl. 45, fig. 11. —TAYLOR, Univ. Kansas Sci. Bull., vol. XXIV, 1936, pp. 507, 525. —DUNKLE and SMITH, Occ. Pap. Mus. Zool., Univ. Michigan, 1937, p. 3 (part). —CLAY, Copeia, 1938, pp. 174-5. —DITMARS, Field Book N. Amer. Snakes, 1939, pp. 159, 220-1. —STEJNEGER and BARBOUR, *Supra*, ed. 4, 1939, p. 130. —TAYLOR, Univ. Kansas Sci. Bull. vol. XXVI, 1940, p. 448, fig. 3. —SMITH, Zoologica, vol. XXVII, 1942, p. 121. —MARTÍN DEL CAMPO, An. Instit. Biol., vol. XII, 1942, p. 761. —CONANT, Amer. Midland Natur., vol. 29, 1943, p. 336. —STEJNEGER and BARBOUR, Bull. Mus. Comp. Zool., vol. XCIII, 1943, p. 163. —SMITH, Proc. U. S. Nat. Mus., vol. 93, 1943, p. 455. —BOGERT and OLIVER, Bull. Amer. Mus. Nat. Hist., vol. 83, 1945, pp. 335, 414.

Some authors have placed *Tropidonotus mesomelanus* Jan (1863, p. 73) in the synonymy of *valida*. The two plates of *mesomelanus* in Jan and Sordelli (1868, pl. V, fig. 3 and pl. VI, fig. 2) clearly indicate, however, that this form is not identifiable with *valida*. The drawings show undivided anal plates, the number of subcaudals is too low for *valida*, and there are also minor differences. Both Ruthven (1908, p. 124) and Smith (1942, pp. 98, 116) consider *mesomelanus* to be a synonym of *Thamnophis melanogaster*.

Type Specimen

The type of *valida* (USNM 1309) is now badly faded but there are faint indications of small dark markings on the scales of the 4th and 7th rows. The belly is immaculate. Complete scale counts and measurements are as follows: Scale rows 19-17, the reduction taking place by the loss of the 4th row of scales on each side at a point above the 78th ventral; ventrals 140; subcaudals 65; upper labials 8, lower labials 10; 1 preocular, 2 postoculars on the left and 3 on the right; anterior temporal on each side fused with the corresponding parietal—3 temporals in the 2nd row and 4 in the 3rd; total length 538 mm., tail length 144 mm.; tail/total length .268; sex ♀.

Body Form

The body in *Natrix valida valida* is moderately slender in juveniles and most adult males and moderately stout in adult females and some of the largest males; the tail is medium slender in both sexes. The head is comparatively long and narrow; in adults of the same total length, it is larger in females than in males. The head is distinctly wider than the neck, the widest part being in the posterior temporal region or at the angle of the jaws. When seen from above the head narrows gradually to the region of the nasal plates; the rostral is broadly rounded. In profile the top of the head is flat, but it curves downward over the prefrontals and internasals. The lower jaw is only slightly recessed into the upper one. The eyes are moderately large and somewhat protuberant; in large specimens the diameter of the eye is less than the distance from the orbit to the nostril, but in the smaller juveniles the two measurements may be the same. The pupil is round.

Dentition

The teeth in *Natrix valida valida* (based on five specimens including three cleaned skulls) are as follows: (1) Maxillary—23 to 25 (24 in seven counts),

increasing in size posteriorly, the last two teeth considerably enlarged. (2) Palatine—12 to 15 (average 13.4), subequal. (3) Pterygoid—24 to 29 (average 25.8), decreasing in size posteriorly. (4) Mandibular—25 to 28 (26 in half the counts), subequal.

Size and Sex

The largest specimen of *valida* I have seen measures 925 mm. in length. It is a female (AMNH 19390 from N. Mazatlán, Sinaloa). The largest male (EHT-HMS 4604 from near Mazatlán) measures 605 mm. in length. Among thirty specimens of *valida* there are seven females which are longer than the longest male. Nine snakes (including both sexes) have incomplete tails; all of those measuring less than 442 mm. have complete tails.

The smallest normal individual (IB from Mazatlán) measures 203 mm. in length;* five others are less than 300 mm. long. No data are available on the size of the newborn young, but, judging from the measurements of the young of other *Natrix* that attain similar adult dimensions, the smallest specimen seen probably was not very old when it was collected and preserved.

Of 30 snakes 11 are males and 18 are females; sex was not determined in one. There are too few specimens to make any definite statement concerning sex ratios, but it is interesting to note that 7 of the 11 males are juveniles whereas 15 of the 18 females may be classified as adults or subadults. Numerous sexual variations are discussed under the headings "Body Form" and "Scutellation."

The tail length in males averages more than 26% of the total length; in females it averages about 25%. Extreme ranges and averages are: Large males (2 specimens) 26.1% and 26.8%, average 26.45%; juvenile males (7 specimens—307 mm. or less) 25.1% to 27.5%, average 26.4%; large females (7 specimens) 23.9% to 26.8%, average 25.3%; juvenile females (3 specimens—339 mm. or less) 23.6% to 25.6%, average 24.4%.

The hemipenis of *valida* is the same as that of *celaeno*; a detailed description of the organ appears on page 264.

Scutellation

The scales of the body are imbricate, strongly keeled, and slightly notched posteriorly. The keels are most prominent on the middorsal rows of scales and less so on the sides of the body. The scales of the first row on each side are somewhat larger than those of the other rows and are only moderately or faintly keeled, or not at all. Some of the scales of the anal region of males bear knobbed keels. Apical pits are lacking.

The scale row formula is usually 19-17, with reduction normally taking place through the loss of the fourth row of scales on each side of the body at a point about opposite the 75th ventral (62nd to 90th). Among the thirty specimens studied, five lose the third row of scales on the left side of the body, instead of the fourth. In six specimens there is a further reduction to sixteen

* See discussion of specimen from El Limoncito on p. 258.

scale rows through the dropping of the middorsal row a short distance anterior to the anus. In four there are 21 scale rows immediately behind the head; in one there are 20. One specimen has 19 rows behind the head, then 21 for a short distance, then 19.

The data on the ventrals may be summarized as follows: Males (10 specimens)—extreme range 141 to 148, interquartile range 142.4 to 145.4, mean $143.9 \pm .68$, coefficient of variation 1.55 per cent. Females (18 specimens)—extreme range 133 to 147, interquartile range 137.8 to 142.8, mean $140.3 \pm .87$, coefficient of variation 2.63 per cent. The coefficient of sexual diversion is 2.53 per cent. The anal plate is divided.

The subcaudals vary as follows: Males (10 specimens)—extreme range 75 to 81, interquartile range 77.0 to 79.4, mean $78.2 \pm .58$, coefficient of variation 2.34 per cent. Females (12 specimens)—extreme range 64 to 76, interquartile range 68.5 to 73.1, mean $70.8 \pm .99$, coefficient of variation 4.85 per cent. The coefficient of sexual divergence is 9.93 per cent. The terminal scale at the end of the tail is short, sharp, and spinelike.

The scales of the head may be described as follows: Rostral twice as wide as high; tongue groove not very deep; underside of rostral with a small crescentic groove paralleling the border of the mouth and running at right angles to the tongue groove. Internasals longer than wide and narrowing considerably anteriorly; prefrontals wider than long and strongly bent downward over the sides of the snout. Frontal nearly transverse anteriorly, slightly concave along its common border with the prefrontals; widest anteriorly, angulate posteriorly, the two arms of the angle at approximately 90° with each other. Supraoculars long and narrow and not projecting above the eye. Parietals not quite so long as their distance from the rostral; broadly in contact, widest anteriorly, and narrowing considerably posteriorly.

Nasals two, the nostril largely in the anterior nasal. Loreal about as long as high or slightly longer than high (loreal fused with the corresponding prefrontal in one specimen). Normally one preocular, twice as high as wide; two preoculars on both sides of the head in two specimens and on one side in one. Postoculars normally three, subequal in size; four on both sides of the head in one specimen, four on one side in another, and two on one side in two others.

Temporals most often 1-2-3; all specimens have one in the first row except the type (USNM 1309) in which each anterior temporal is fused with the corresponding parietal, and one other (IB) in which a small narrow scale is wedged between each anterior temporal and the corresponding 6th upper labial. In the second row there are either 2 (43 counts) or 3 (17 counts); in the third row there are 2 (1 count), 3 (46 counts), or 4 (9 counts).

Upper labials 7 to 9, the distribution in a total count of 60 is 7 (1), 8 (57), and 9 (2); 6th the largest, the fourth and fifth entering the eye. Lower labials 9 to 11, the distribution in a total count of 60 is 9 (1), 10 (55), and 11 (4); 6th the largest, the first pair meeting on the midventral line; first five on each side in contact with the corresponding anterior chin shield.

Mental triangular. Posterior chin shields longer than the anterior ones. Posterior ones separated from each other by the width of one narrow scale

anteriorly and by two scales posteriorly; two to four small scales between the first ventral and the last lower labial.

Coloration and Pattern

The dorsum in *valida* is uniform light grey or pale olive grey marked with numerous small, irregular spots of black or very dark brown. The degree of spotting varies; in some individuals the markings are very small and are scarcely noticeable unless the skin is stretched; in others they are conspicuous and impart a pattern suggestive of some of the spotted varieties of *Thamnophis*. The markings, in most cases, lie on the antero-lateral portions of individual scales where they frequently take the form of a small "V" with the angle toward the head of the snake; in no case does any single dark spot involve an entire scale. There is a tendency for the markings to occur most frequently (or most conspicuously) on scales of the 4th or 5th, and of the 7th or 8th rows, making the spots appear to be in four rows, two on each side of the body. Actually, they may appear on any of the dorsal scales. Normally they are larger and more prominent in the middorsal region than they are on the sides of the body; likewise they are most conspicuous on the anterior part of the body and least so posteriorly. In a number of individuals the two lowermost rows of scales on each side of the body are slightly paler than those above, thus faintly suggesting lateral stripes like the ones so prominent in dark specimens of *celaeno*.

The tail normally is unmarked and of the same tone as the ground color of the body.

The belly usually is uniform yellow, yellowish grey, or cream-colored, although in some specimens, particularly in large ones, the general color may be indistinctly diffused with a darker and greyer tone, at least on the antero-lateral portions of the ventral scutes; rarely it may produce a spotted or mottled effect. The dark coloration, if present, usually becomes more general and more intense toward the posterior end of the body and on the under side of the tail. In specimens having uniformly light bellies the under surface of the tail also may be uniformly light, except that there may be a slight concentration of dark pigment along the midventral line.

The top and sides of the head are uniform olive grey or with faint suggestions of a slightly darker pattern. Each of the parietals, in juveniles and some adults, bears a rather faint, somewhat elongated light spot along their common suture; these are similar to the parietal spots which are conspicuous in many other snakes—especially members of the genus *Thamnophis*. The labials are uniform yellow or yellowish olive; the upper ones and the posterior lower ones are often darker than the rest of the lower ones. The sutures between the upper labials, excepting the one separating the last two (which is unmarked) are usually outlined with black; the sutures between the lower labials are similarly but less completely or intensively marked. In juveniles there is a yellowish area (bordering the eye) on each preocular, and often there is another smaller one involving the lowermost postocular. These light markings sometimes also may be seen on large individuals. The chin and throat are uniform yellow or cream.

Juveniles, in general, are paler and more conspicuously marked than adults.

One snake (EHT-HMS 4982 from near Tepic, Nayarit), which resembles other specimens of *valida* in almost all respects, is unique in possessing a distinct, light greyish-yellow dorsal stripe. This involves the middorsal row of scales and small fractions of the adjacent rows; it begins two scales behind the posterior angle of the parietals and disappears on the tail a few scales behind a point directly above the anus. In this snake the two lowermost rows of scales are slightly lighter than the rest of the dorsum and the parietal spots are readily discernible. If it were not for its divided anal plate and the fact that all other details check with *valida*, this snake could readily pass as a *Thamnophis*. Its total length is 525 mm., but a part of the tail is missing. The only other specimen from near Tepic (EHT-HMS 4984) is normally patterned. It was collected on the same day as the striped one. It would be of interest to see a series of specimens from this locality.

Taylor (1940, 448-50) has published a description and drawings of an anomalous juvenile from El Limoncito, Guerrero (EHT-HMS 19224). This snake differs from other young specimens of *valida* in some details of scutellation and it also differs in head shape and pattern. The nostril is pierced in the center of a single nasal scute instead of lying between two scutes (there are slight traces of grooves running from the edges of the nasal plate to the nostril). There are only nine lower labials on each side of the head—another unusual condition. The head, in general, is proportionately smaller and less elongated than in typical juveniles of *valida*. All the dark dorsal markings are indistinct and only slightly darker than the general ground color; the spots on the fourth row of scales are basically similar in shape to those of typical *valida*.

The scale counts and measurements may be summarized as follows: Scale rows 21-19; reduction takes place by the loss of the 6th row of scales above the 76th ventral on the left side and above the 74th on the right. Near midbody the dorsal scales are somewhat abnormal—small, anomalous scales being present at irregular intervals. Ventrals 133; subcaudals 72; upper labials 8; lower labials 9; oculars 1-3; temporals 1-2-3; total length 181 mm.; tail length 45 mm.; tail/length 24.9%; sex ♂.

The peculiarities of this specimen may be interpreted in either of two ways:

1: It is an aberrant juvenile which, like so many newborn snakes, exhibits abnormal characteristics. In all probability it would not have survived in nature. Dunn, Inger, and other authors have commented upon the considerable amount of departure from the normal which is often manifested in juvenile snakes.

2: It exhibits evidences of specific or subspecific divergence, and, if similar serpents are found in the same general area, they may be regarded as constituting a new form, probably racially allied to *valida*.

This snake shows a general reduction in scale characters. In addition to the single nasal scute and the fewer number of lower labials, it exhibits the lowest number of ventrals (133 compared with 141), the lowest number of subcaudals (72 compared with 75), and the shortest tail (24.9% compared with 25.1%) of any male specimen of *valida*.

El Limoncito is at the extreme southern edge of the known range of *valida*.

There is a general tendency for the number of ventrals in *valida* to be fewer toward the south. Two females from Colima and a female from Laguna Coyuca, Guerrero, have 133, 135, and 135 ventrals, respectively. These are the lowest counts for any specimens of *valida*.

When more material from Guerrero is available for study it should shed considerable light upon the situation.

I have not included this specimen in the general summarizations of scale counts, measurements, etc.

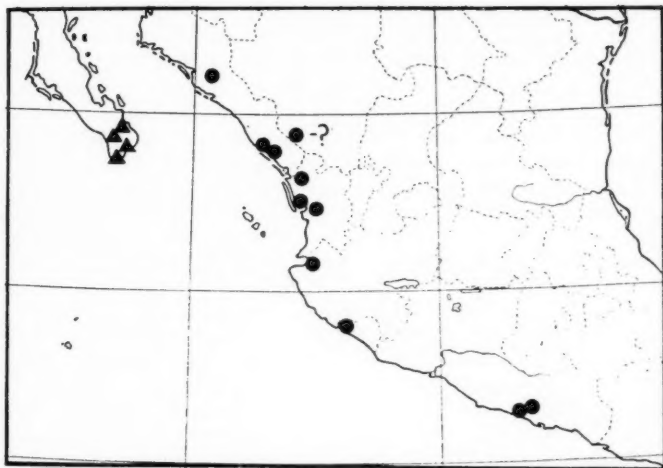


Fig. 2. Distribution of *Natrix valida valida* (circles) and *Natrix valida celaeno* (triangles). The question mark indicates that the exact locality in Durango is unknown; on physiographic grounds it probably is in the extreme western part of the state. (Base map courtesy of Chicago Natural History Museum).

Range

Natrix valida valida occurs in the coastal lowlands of western Mexico from central Sinaloa to central Guerrero. Specific locality records are:

COLIMA: (USNM 31384)*; Manzanillo (AMNH 19590).

DURANGO: (USNM 1309).

GUERRERO: El Limoncito (near Venta Vieja, NE of Acapulco) — EHT-HMS 19224; Laguna Coyuca (UMMZ 80938).

JALISCO: Las Peñas, Vallarta (AMNH 19307).

NAYARIT: Acaponeta (AMNH 62278, 62283-96); San Blas (Cope, 1887, p. 74 and Dugés, 1896, p. 481); near Tepic (EHT-HMS 4982, 4984).

SINALOA: Culiacán (AMNH 62279-80); Mazatlán (EHT-HMS 4604-5; 1B); N. Mazatlán (AMNH 19390); Presidio (Boulenger 1893, p. 238); 10 mi. S of Presidio (EHT-HMS 4602-3).

Abbreviations refer to museums. For full explanation see p. 272.

In all probability USNM 31384 and USNM 1309 are from the states of Colima and Durango, respectively, and not from the cities of the same names. Both snakes were collected many years ago when detailed locality data were not considered essential. Since all the definite records for this subspecies are from the coastal plain, it is reasonable to presume that these two specimens also came from the same region or from along the rivers which flow into it. The only other Colima record is from Manzanillo, which is on the coast and below the 100-meter contour. Although Durango is an inland state, there are several parts of its extreme western portion which are less than 200 meters in elevation.

This snake also has been reported from other localities either erroneously or ambiguously. Such records are from:

1: Rabeh Valley, Utah. Van Denburgh (1922, p. 786) has called attention to the fact that a snake recorded by Cope from this locality as *valida* (USNM 4650) actually is a *Thamnophis ordinoides vagrans* with a divided anal plate. I have examined this specimen and agree with Van Denburgh.

2: Rio San Pedro, midway between Chihuahua and Naica, Chihuahua. Dunkle and Smith (1937, p. 3) based this record on a specimen in the Taylor-Smith collection (EHT-HMS 5408). This snake, which has a single anal plate, is actually a *Thamnophis*. Dr. Smith, at my request, has reexamined it and identified it as *T. rufipunctatus*.

3: Sonora. Cope (1892, p. 670) mentions Sonora in stating the range of *valida* but gives no specific locality. Possibly he may have been referring to his "Sonoran Province" since he included *valida* in his paper (1867) on the herpetofauna of the "Sonoran Province of the Nearctic Region." There are no specimens extant from the state of Sonora, but, as Bogert and Oliver (1945, p. 414) have pointed out, it is possible that *valida* may be found within its borders, perhaps in the drainage of the Rio Fuerte or even the Rio Mayo.

The vertical distribution of *valida* varies from virtually sea level to at least two hundred meters, although, in view of the almost complete lack of altitudinal data, it may occur at somewhat greater elevations. The localities for most specimens, unfortunately, are given simply as the nearest towns. Thus, at least one of the two snakes from Tepic actually was collected along a tributary of the Rio Grande de Santiago, probably at a much lower altitude than the city. Tepic itself, which lies at the top of an escarpment, is at an elevation of 952 meters.

Habitat and Habits

Like other members of its own genus and like most of the species of *Thamnophis* that inhabit semi-arid regions, *Natrix valida valida* apparently is found only in or near bodies of water. Taylor (in correspondence) states that he collected specimens (1) near the edge of a small pool ("perhaps only a rain pool"); (2) in the open near a pool that was nearly dry; and (3) in an "open lot near the house." In the last-mentioned locality there was a tiny ox-bow pond and a tiny stream within a hundred yards. He also found a specimen "in water at night . . . swallowing a *Rana pipiens*." Another snake was

caught about a hundred yards from the Río del Presidio. Bogert has told me that he did not see *valida* actually in water, but that he collected individuals at the edge of a stream after a flood had receded and also found them under rocks and debris along another stream. Both of his localities (near Acaponeta and Culiacán) are in the coastal plain at the foot of the mountains.

Specimens in the American Museum of Natural History, collected by Paul D. R. Rühlhing, bear the following brief field notes: "On bush above water; under canoe on beach; in a house."

There is little to record on habits. Both Bogert and Taylor agree that specimens of *valida* are not very aggressive and that their actions in general are similar to those of garter snakes. Taylor did not see them swim or take refuge in water. They were not particularly elusive; they manifested no special methods of escape and Taylor says, "I caught *all* I saw." Bogert found their musk to be much like that of other species of *Natrix*.

The stomachs of two specimens contain the remains of frogs; identifiable in one case as *Leptodactylus melanonotus*. Bogert saw specimens of *valida* with frogs of the same species in their mouths.

Nothing is known about the breeding habits of *valida*.

NATRIX VALIDA CELAENO (Cope)

Synonymy

1860. *Tropidonotus celaeno* COPE, Proc. Acad. Nat. Sci. Philadelphia, vol. XII, p. 341. (Type locality Cabo San Lucas, Baja California, Mexico. Type specimen USNM 5281a). — COPE, *Id.*, vol. XIII, 1861, p. 298.

1860. *Tropidonotus tephroleura* COPE, *Id.*, vol. XII, p. 341.

1861. *Tropidonotus validus* COPE, *Id.*, vol. XIII, pp. 298, 305. — COPE, *Id.*, vol. XVIII, 1867 [1866], pp. 310-2. — BOULENGER, Cat. Snakes Brit. Mus., vol. I, 1893, p. 237. — GÜNTHER, Biol. Centrali-Amer., 1894, p. 134. — MOCQUARD, Nouv. Arch. Mus. Hist. Nat., 4th Ser., vol. I, 1899, p. 329. — DITMARS, Reptile Book, 1907, p. 245, pl. LXXIII, fig. 11. — WERNER, Zool. Jahrb., vol. 57, 1929, p. 26.

1875. *Tropidonotus validus validus* COPE, Bull. U. S. Nat. Mus., I, p. 42. — YARROW, *Id.*, 24, 1882, p. 132. — BELDING, West Amer. Sci., vol. III, 1887, p. 99.

1875. *Tropidonotus validus celaeno* COPE, Bull. U. S. Nat. Mus., I, p. 42. — YARROW, *Id.*, 24, 1882, p. 133. — BELDING, West Amer. Sci., vol. III, 1887, p. 99.

1882. *Tropidonotus validus tephroleura* YARROW, Bull. U. S. Nat. Mus., 24, p. 133. — BELDING, West Amer. Sci., vol. III, 1887, p. 98.

1883. *Tropidonotus leberis validus* GARMAN, Mem. Mus. Comp. Zool., vol. VIII, pp. 28, 143.

1884. *Regina valida* GARMAN, Bull. Essex Inst., vol. XVI, p. 24.

1887. *Regina valida valida* COPE, Bull. U. S. Nat. Mus., 32, p. 74.

1887. *Regina valida celaeno* COPE, *Id.*

1892. *Natrix valida valida* COPE, Proc. U. S. Nat. Mus., vol. XIV [1891], p. 670. — COPE, Rep. U. S. Nat. Mus., 1900 [1898], p. 984, fig. 259.

1892. *Natrix valida celaeno* COPE, Proc. U. S. Nat. Mus., vol. XIV [1891], p. 670. — COPE, Rep. U. S. Nat. Mus., 1900 [1898], p. 986, fig. 260.

1896. *Natrix valida* VAN DENBURGH, Proc. California Acad. Sci., Ser. 2, vol. V, p. 152. — STEJNEGER and BARBOUR, Check List N. Amer. Amph. & Rept., ed. I, 1917, p. 97. — VAN DENBURGH and SLEVIN, Proc. California Acad. Sci., Ser. 4, vol. XI, 1921, pp. 52, 68. — SCHMIDT, Bull. Amer. Mus. Nat. Hist., vol. XLVI, 1922, p. 693. — VAN DENBURGH, Rept. Western N. Amer., California Acad. Sci., 1922, p.

784. — NELSON, Nat. Acad. Sci., vol. XVI, 1922, pp. 114-5. — STEJNEGER and BARBOUR, *Supra.* ed. 2, 1923, p. 109. — BLANCHARD, Pap. Michigan Acad. Sci. Arts Lett., vol. IV, 1925, p. 12. — LINSDALE, Univ. California Publ. Zool., vol. 38, 1932, p. 380. — STEJNEGER and BARBOUR, *Supra.*, ed. 3, 1933, p. 118. — DITMARS, Rept. N. Amer., 1936, p. 161, pl. 45, fig. 11. — CLAY, *Copeia*, 1938, pp. 174-5. — DITMARS, Field Book N. Amer. Snakes, 1939, pp. 159, 220-1. — STEJNEGER and BARBOUR, *Supra.*, ed. 4, 1939, p. 130. — STEJNEGER and BARBOUR, Bull. Mus. Comp. Zool., vol. XCIII, 1943, p. 163. — BOGERT and OLIVER, Bull. Amer. Mus. Nat. Hist., vol. 83, 1945, p. 335.

1896. *Natrix celaeno* VAN DENBURGH, Proc. California Acad. Sci., Ser. 2, vol. V, p. 154.

Type Specimen

Cope based his *Tropidonotus celaeno* on "One specimen (No. 351) discovered by Mr. John Xantus at Cape St. Lucas, Lower California, and deposited in the Museum of the Smithsonian Institute." There are now seven specimens of *celaeno* in the National Museum with these data and all agree in coloration with Cope's description. All seven snakes have the same catalogue number—USNM 5281—but only one (USNM 5281a) agrees in every detail of scutellation. This may be regarded as the type. A parchment tag, with "No. 351" on it, is loose in the jar.

Attention should be called to the fact that a small specimen in the collection of the Academy of Natural Sciences of Philadelphia (ANSP 6644) also matches Cope's description exactly (Cope failed to include measurements). This snake, besides bearing the metal tag no. 6644, has a small paper tag attached to it with the number 5281—so also has ANSP 6643. These two snakes evidently belonged to the same series as the seven National Museum specimens. Their presence in the Academy collection is readily explainable. Cope had in his possession, at the time of his death, a large number of specimens from the Smithsonian Institution. After Cope's demise Dr. Leonhard Stejneger examined the borrowed material, returned some of it to Washington, and permitted the remainder to go to the Academy. Presumably ANSP 6643-4 were among the lot. It is also safe to presume that they had been borrowed by Cope at an early date, otherwise their paper tags would have been replaced by metal tags at the time (during the late 1870's) when the Smithsonian collection was reorganized.

Complete scale counts and measurements for USNM 5281a are as follows: Scale rows 21-19-21-19-17, the changes in numbers being occasioned by the loss or addition of the 4th row of scales in every case—except the increase from 19 to 21 where the 5th row is involved; ventrals 145; subcaudals 71; upper labials 8, lower labials 10; 1 preocular, 3 postoculars; one anterior temporal on each side, temporals of second row—3 on left and 2 on right, temporals of third row—4 on left and 3 on right; total length 524 mm., tail length 128 mm.; tail/total length .244; sex ♀.

Body Form

In its general body proportions, shape and size of head, etc., *celaeno* does not differ in any significant manner from *valida*, and the description of the latter will serve equally well for *celaeno*.

Dentition

The teeth in *Natrix valida celaeno* (based upon the study of ten specimens, including three cleaned skulls) are as follows: (1) Maxillary—24 to 27 (26 in exactly half of the counts), increasing in size posteriorly; the last two teeth are twice or nearly twice as large as the others. Occasionally the third from the last tooth and, rarely, the fourth from the last may be somewhat enlarged. (2) Palatine—13 to 15 (14 in fourteen counts), subequal. (3) Pterygoid—25 to 31 (normally 26 or 27), decreasing in size posteriorly. In some snakes the last few pterygoids are much smaller than the others. (4) Mandibular—27 to 30 (average 28.2), subequal (slightly smaller posteriorly in one specimen).

Size and Sex

From the evidence at hand it appears that male and female specimens of *celaeno* may attain approximately the same size. The largest individual examined is a female measuring 970 mm. in length—a small part of its tail is missing; this snake is NHSSD 17655 from San José del Cabo. The largest male measures 955 mm. (USNM 4683a from Cabo San Lucas). The next ten largest specimens (in descending order) measure as follows: 945 mm. (♀), 917 (♀), 886 (♀), 874 (♂), 850+ (♂), 842 (♂), 832+ (♂), 790+ (♀), 760 (♂), and 760 (♀).

The sixteen smallest juveniles with perfect tails measure 233 to 260 mm. (average 244 mm.) in total length. These, in all probability, are young of the year, and it is conceivable that they may represent the average size of newborn young of *celaeno*. Two apparently full-term embryos, however, which were removed from the female measuring 917 mm., are approximately 195 and 200 mm. long. Conceivably, these might have grown longer before birth, but their measurements compare favorably with the smallest known specimen of *valida* (203 mm.). Since there were only two embryos and since most *Natrix* litters contain a greater number of young, it is probable that the female may have been caught after giving birth to part of her family. If this were true, then it would indicate that the embryos were completely formed and ready to be extruded. There is no evidence to bear this out, other than that the two fetal snakes occupied only a small part of the abdominal cavity of the mother; there was ample room for many more. Other large females caught about the same time in the same or nearby localities contained no embryos and apparently already had given birth to their young.

Of the snakes examined, 47 are males and 48 are females; sex could not be determined in two. Among the only large series of specimens taken in a single locality and all about the same time (Agua Caliente, July 23 to 25, 1919) 26 are males and 23 are females. From these data it can be inferred that the two sexes may occur in approximately the same numbers in nature.

The tail length in males averages about 26% of the total length; in females it averages about 25%. Extreme ranges and averages are: Large males (25 specimens) 24.6% to 28.3%, average 26.3%; juvenile males (13 specimens—284 mm. in length or less) 24.8% to 27.2%, average 26.1%; large females (24 specimens) 23.5% to 25.7%, average 24.8%; juvenile females (15 specimens—

304 mm. or less) 23.9% to 26.0%, average 25.2%. Tail length ratios could not be computed for 20 specimens. Of these 18, including several juveniles, have incomplete tails.

Hemipenes

Each hemipenis, when everted, is bilobed at its distal end and furnished with a smooth, saccular tip. The sulcus is simple and it terminates in the depression between the lobes. Most of the organ is thickly covered with small spinules which diminish in size distally. There is one large basal spine (2 or 3 mm. long in snakes measuring 500 to 731mm.) lateral to the sulcus and followed by a somewhat smaller spine and two much smaller ones. On the opposite side of the sulcus, in a slightly more distal position, is a single enlarged spine somewhat smaller than the basal spine. The shaft of the organ, on the side opposite the sulcus, is smooth throughout an area occupying nearly as much space as the enlarged spines; proximal to this area are numerous spinules.

In situ the hemipenis extends caudally to a point about opposite the tenth subcaudal (ninth to twelfth in five specimens) and the retractor penis muscle inserts at the level of the twenty-third to the twenty-eighth subcaudal.

Scutellation

The scale characters of *celaeno*, in the main, are the same or very similar to those of *valida*. The dorsal scutes exhibit the same degree of carinations: males have knobbed anal keels. Apical pits are lacking, although in a few large adults there appear to be slight depressions on many of the scales in the positions where pits are prominently in evidence in other species of *Natrix*. The pits are most readily seen in live water snakes; it has been impossible to check this character on living specimens of either *valida* or *celaeno*.

The scale row formula normally is 21-19-17 (in 41% of the specimens examined) or 19-17 in (32%). In the majority of individuals of the first group there are 21 rows only for a short distance behind the head, but in others the decrease to 19 rows occurs farther back—as far posteriorly in one snake, as a point above the 63rd ventral. The reduction usually takes place through the loss of the 5th row of scales on each side of the body, but sometimes the 4th rows are dropped, or the 5th on one side and the 4th on the other. Reduction from 19 to 17 rows almost always occurs through the loss of the 4th row on both sides; occasionally the 3rd row may be dropped instead, either on both sides or on one. The reduction from 19 to 17 may occur from above the 76th ventral to as far back as the 111th; there is a marked tendency for it to occur farthest back in those snakes which have 21 rows of scales on the anterior third or more of the body.

Sexual differentiation in the dorsal scale counts is notable. Females, on the average, have the greater number of rows. Among 39 snakes with the formula 21-19-17 there are 27 females and only 12 males; among the 30 with the formula 19-17 there are 25 males and only 5 females. The greater number of rows probably is correlated with greater girth, which provides more room for the developing young. This same relation is known to occur in numerous other species of snakes.

Only females have more than 21 rows and only males have less than 17. One female has a count of 23 rows for a short distance and two others have 22; in these three snakes and in several others the dorsal scutes are arranged in such irregular fashion that the rows increase and decrease several times and counting is difficult. Three male snakes drop the middorsal row of scales so that there is a total of 16 rows just anterior to the anus; a count of 15 rows posteriorly occurs in one juvenile male.

Ventral scale counts may be summarized as follows: Males (47 specimens)—extreme range 138 to 149, interquartile range 142.9 to 145.7, mean $144.3 \pm .30$, coefficient of variation 1.42 per cent. Females (48 specimens)—extreme range 136 to 148, interquartile range 142.0 to 144.8, mean $143.4 \pm .31$, coefficient of variation 1.50 per cent. The coefficient of sexual divergence is .63 per cent. The anal plate is divided.

Subcaudal counts vary as follows: Males (39 specimens)—extreme range 74 to 81*, interquartile range 76.8 to 79.0, mean $77.9 \pm .26$, coefficient of variation 2.08 per cent. Females (39 specimens)—extreme range 67* to 75, interquartile range 69.5 to 73.5, mean $71.5 \pm .48$, coefficient of variation 4.15 per cent. The coefficient of sexual divergence is 8.57 per cent. The terminal scale at the end of the tail is short, sharp, and spinelike.

Such normally nonvarying scales as the rostral, frontal, parietals, nasals, mental, chin shields, etc., are identical with the corresponding scales in *valida* and descriptions of them need not be repeated. Scales which vary in number are discussed below.

Usually a single preocular; two preoculars on each side in 2 specimens and one on one side and two on the other in 7 specimens. Postoculars normally three; three on both sides in 67 snakes, two on both sides in 9, two on one side and three on the other in 17 snakes, four on both sides in 1, and two on one side and one on the other in 3. Most departures from the normal are occasioned by the fusing of the upper one or two postoculars with the supraocular; in one instance the uppermost postocular is fused with the corresponding parietal.

Temporals are most often 1-2-3; all specimens examined have one in the first row. In the second there are 1 (1 count), 2 (185 counts), or 3 (5 counts); in the third row there are 1 (6 counts), 2 (77 counts), 3 (89 counts), or 4 (5 counts). In a few instances various temporal scales are fused with each other, such as the anterior temporal with the lower temporal of the second row, the three scales of the third row fused together irregularly, etc.

Upper labials 7 to 9, the distribution in a total count of 193 being 7 (6), 8 (185), 9 (2); 6th the largest, the 4th and 5th entering the eye. Lower labials 9 or 10, the distribution in a total count of 193 being 9 (7), 10 (186); 6th the largest, the first pair meeting on the midventral line; first five in contact with the anterior chin shields.

* Van Denburgh and Slevin (1921, p. 69) have listed three individuals with subcaudal counts beyond the extremes here indicated; these they give as 83, 82, and 65, respectively, and they identified all as females. My counts on these same specimens are 80, 79, and 74, and all are actually males. Van Denburgh (1896, p. 152) has also recorded a subcaudal count of 82.

I have sorted the specimens of *celaeno* into two lots according to pattern—those similar to mainland *valida* (Groups A and B—see below) and those that are typically dark (Groups C and D). Mathematical summations of the ventrals and subcaudals indicate that there are no significant differences in the two lots of specimens; the means and extremes are almost the same in both cases. Nor do there appear to be any significant variations in other scale characters.

Coloration and Pattern

As outlined on page 251, specimens of *celaeno* may be sorted into four pattern groups. These may be diagnosed and described as follows:

GROUP A. *Light colored snakes indistinctly marked with small dark spots.*

Such snakes are indistinguishable from mainland *valida* (see description of that species). The dorsal ground color is uniform light grey or light greenish grey; the top and sides of the head are more or less uniform light olive grey; the labials are yellow except along the sutures where they are edged with black.

GROUP B. *Light colored snakes conspicuously marked with dark spots.*

There is considerable variation among snakes of this group; some have the dark dorsal markings only a little more prominent than they are in snakes of Group A, but others present a very spotted appearance. Basically, however, the patterns of all members of this group are similar. The dorsal ground color usually is light grey or greyish green; in some specimens it may be brownish. The dark markings are larger or much more numerous (or both) than they are in snakes of Group A, and the most conspicuous spots may occur on any of the upper dorsal rows of scales instead of being more or less confined to certain definite longitudinal rows. Usually the dark markings are faint or lacking entirely on the first three rows of scales on each side of the body. The chin, throat, and belly normally are light and unpigmented, but in some snakes, particularly in large ones, the general coloration of the belly may be suffused with a darker and greyer tone. The top and sides of the head usually are uniform olive grey; the labials are yellow except along the sutures where they are edged with black.

GROUP C. *Dark snakes with black heads; dorsal surfaces with some indications of pattern; a light lateral stripe involving the first three rows of scales.*

Each snake of this group is patterned with large black or dark brown lateral spots which are two to four scales in width and four or five scales high. Anteriorly the spots are more or less distinct and a ground color of medium grey or grey brown appears between them. Throughout most of the body, however, they are confluent with one another and the ground color is greatly suppressed and may be visible only here and there. Down the center of the back is a black or very dark brown area two or three scales in width. This is uncrossed by the ground color, and, throughout most of its length, it is more or less confluent with the adjacent dark spots. In some individuals the lateral spots run together to form a wide, irregular dark stripe indistinctly separated from the dark middorsal area by small irregular bits of ground color. Such snakes have the appearance of being marked with three dark, irregular, and poorly defined longitudinal stripes. The dark and light markings may be continued on the tail or that appendage may be uniform dark.

On each side of the body is a lateral stripe of grey or light brown. This usually involves the second row of scales and parts of the first and third rows; occasionally it encroaches upon scales of the fourth row. The upper and lower edges are ragged and irregular so that the stripe varies in width. On its upper edge it is bordered by the dark lateral spots; on its lower edge it is bordered by dark pigment on scales of the first (and sometimes the second) row of scales and the edges of the ventrals. This pigment may be as dark as that of the dorsal spots, but it is usually lighter; in some snakes it is slightly darker than the general coloration of the belly, in others it may match the belly in general tone.

The head is uniform black above except for a conspicuous grey spot on the 6th upper labial; there also may be small, irregular grey areas on the other labials, chiefly along the commissure. The chin and throat are black or dark brown, except that the edges of some of the scales may be light brown; in some snakes there are small, irregularly arranged spots of yellow or light brown on the chin and throat.

The belly is mostly dark. Anteriorly it is similar to the throat but farther back it is brown or medium grey, heavily stippled or suffused with dark grey or dark brown. The underside of the tail may be similar or somewhat darker than the anterior part of the abdomen.

GROUP D. *Dark snakes, uniformly black or dark brown above and below — except for a light lateral stripe on each side of the body.*

Snakes of this Group are essentially like those of Group C except that they are uniform black or very dark brown above, hence there are no indications of spots or of a light dorsal ground color. The lateral stripe of light brown or grey involves the first three rows of scales (sometimes the fourth) and is irregular along both its upper and lower edges. The head is uniform black, except for a grey area on the 6th upper labial and (occasionally) smaller grey areas on other labials, chiefly along the commissure. The chin and throat normally are black except for faint indications of light pigment in some specimens. The belly is essentially dark, but posteriorly it is medium grey or grey brown, heavily stippled and suffused with darker brown or grey. The underside of the tail is similar but usually is darker than the posterior part of the belly.

There is a complete overlapping of pattern characteristics between snakes of Groups A and B and between snakes of Groups C and D. At least two specimens (USNM 37545—♂ and 12642e—♀) are intermediate between Groups B and C (see page 251).

Disregarding these two individuals (and one of Group A in which the sex could not be determined) the remaining 94 specimens may be sorted by sex and pattern as follows:

	Males	Females
Group A	6	6
Group B	7	10
Group C	4	19
Group D	30	12

The sex ratios are approximately the same in the small samples belonging to Groups A and B, but they are significantly unequal in the larger samples of Groups C and D. It is apparent in the last two groups that males tend to be darker in coloration than females. Thirty of the 34 males (88%) bear the very dark pigmentation of Group D, whereas 19 of the 31 females (61%) show the evidences of pattern which are characteristic of snakes of Group C.

Since a number of the specimens tabulated above show evidences of fading from long preservation, it is probable that several classified in pattern Group C originally may have belonged in Group D. Therefore, the large series of specimens in the collection of the California Academy of Sciences, obtained by Joseph R. Slevin in 1919, was examined separately. These snakes, all preserved at approximately the same time and in the same manner, show even more strikingly the tendency for males to be darker than serpents of the other sex. Nine of the Slevin snakes are classifiable in Group A (2♂; 1♀) or Group B (2♂; 4♀). All other males (24) belong to Group D, and 13 of 22 females (59%) belong to Group C; 9 females belong to Group D.

There are juveniles and large adults (as well as individuals of intermediate sizes) belonging to all of the several pattern groups, hence there is apparently no general ontogenetic darkening and obscuration of pattern, such as is known to occur in other species of snakes (in *Natrix e. erythrogaster*, for example). The prevalence of dark coloration among males, however, may be indicative of a tendency for snakes of this sex to become darker with age. If broods of young could be secured and raised in captivity much light would be shed on this and other matters which are now only open to conjecture.

Another point of interest that will not be settled until more material comes to hand is the fact that the ratio of dark specimens (Groups C and D) to light specimens (Groups A and B) may not be the same near the coast as it is in areas of high elevation. A clue to such a possibility is furnished by Van Denburgh (1896, pp. 152-5) who recognized two distinct species of water snakes in Baja California, obviously assigning light specimens to *Natrix valida* and dark ones to *Natrix celaeno*. He recorded both forms from San José del Cabo, but light ones from that locality were much more numerous than dark ones. Unfortunately the snakes upon which he based this report were lost in the San Francisco earthquake and fire of 1906. In the material collected in upland localities (chiefly at Agua Caliente) by Slevin, dark snakes greatly predominate. Such diverse pattern ratios may be the result of the vagaries of collecting; on the other hand they may indicate some correlation between elevation and pigmentation. King (1939) and Netting (in manuscript) have shown that certain snakes (*Thamnophis sirtalis sirtalis* and *Storeria occipitomaculata occipitomaculata*) have a tendency to be black or very dark in certain areas of high altitude in the United States.

Range

Natrix valida celaeno has been found only in the Cape Region of Baja California. Locality records are as follows:

BAJA CALIFORNIA: Agua Caliente (CAS 45890-923, 45925-39; MCZ 13160; MVZ 11909-11); Cabo San Lucas (ANSP 6641-4; USNM 4683a-f, 5281a-g); Miraflores (AMNH 5605; CAS 45940-1; CNHM 25873-5); Río San José (USNM 12642a-e*); San José del Cabo (AMNH 5573, 5583; CAS 45944-5; MCZ 6818; MVZ 11907-8; NHSSD 17655; USNM 37545, 56181-2, 64582); Santiago (CAS 45942-3).

No detailed altitudinal data accompany any of the specimens of *celaeno*. According to the map, "Baja California Sur," published by the American Geographical Society, Agua Caliente is at an elevation of approximately 700 meters, Miraflores and Santiago are each at 400 m., and the town of San José del Cabo is at 100 m. The Río San José empties into the sea near San José del Cabo and Cabo San Lucas is on the coast. Much of the material sent to American museums in the early days which was labelled San José del Cabo and Cabo San Lucas undoubtedly was collected in other parts of the Cape Region.

* These snakes, catalogued and reported from La Paz, actually are from the Río San José according to Van Denburgh (1922, p. 787).

Habitat and Habits

Joseph R. Slevin, who collected the majority of the specimens of *celaeno*, writes (in correspondence) as follows:

Agua Caliente, where most of the series came from, is a small village fairly well south of La Paz and situated in somewhat hilly country. There is a permanent stream flowing through a small rocky canyon and it was from the stream that the snakes were taken. Santiago is the same type of country. Miraflores is a little more level but all three localities are typical Mexican desert country.

Van Denburgh and Slevin (1921, p. 68), commenting upon the same snakes, state:

Most of the specimens were collected in a stream flowing from the base of Mount San Rafael near Agua Caliente. Individuals were abundant in the quiet waters along the sides of the stream, where they were feeding on pollywogs, probably of *Bufo punctatus*, which swarmed in every pool. Only one specimen was found at any distance from the water, and this one only a hundred yards or so.

Cope (1861, p. 298), in writing about specimens from Cabo San Lucas, remarked that "According to Mr. Xantus (John Xantus, collector of the types of *celaeno* and *tephropleura*) they are most common in swampy meadows among long grass." Some of Xantus' specimens came from the Río San José, according to his own field notes.

Natrix valida celaeno may be expected to occur along many of the permanent and semi-permanent streams of the Cape Region. Slevin found it to be by far the most common snake in the upland country near Agua Caliente, and Van Denburgh, writing about a collection from near the coast (1896, p. 153), states, "It appears to be the most abundant snake of the country immediately surrounding San José del Cabo."

The available data indicate that specimens of *celaeno*, like other water snakes, subsist largely upon fish and amphibians. Van Denburgh (*op. cit.*, p. 154) notes that "Some of the specimens contained small fish, *Mugil brasiliensis*."

The stomachs of the great majority of the snakes of the Agua Caliente series contain toadlets or nearly transformed tadpoles of *Bufo punctatus*. A few also have toads in their throats. The toadlets have head-body lengths of 9 or 10 mm.; the head-body lengths of the tadpoles are the same and many have tails 6 mm. long. Sixteen toadlets were removed from the throat and stomach of a snake 520 mm. long—also a nymphal roach 6½ mm. long. One of the snakes in the collection of the Chicago Natural History Museum has a medium-sized *Bufo punctatus* in its mouth. Many of these snakes have heavy infestations of ascarids in their stomachs and esophaguses which have been identified as *Ophidascaris* sp. by Dr. E. W. Price, Agricultural Research Administration, U. S. Department of Agriculture.

Nothing is known about the breeding habits or birth of young, except the finding of two full-term embryos in a large female as noted in the section above on Size and Sex.

Comments Upon Distribution

The distribution of the two races of *Natrix valida* might seem, at first glance, to be difficult to explain. The mainland subspecies, *valida*, has a fairly continuous range through several hundred miles of Mexico's west coast; eventually it may be found along almost all the water courses of the region. It is essentially a snake of the lowlands, and the present limited information indicates that it ascends only a little way (if at all) into the mountains that mark the inner boundary of a narrow coastal plain.

On the other hand, *celaeno* is restricted to the relatively small, isolated Cape Region of Baja California. This area is bordered everywhere by salt water except on the northwest where arid conditions prevail. Certainly *celaeno* can have no direct contact with *valida* at present, for the likelihood of specimens crossing from the mainland (or vice versa) is extremely remote. In addition to the obvious hazards of negotiating a hundred miles of open sea, there is the fact that any aquatic snake making a landfall would be apt to come ashore on a dry and inhospitable coast, where conditions would be unsuited for its survival.

According to Nelson (1922) the mountainous portion of the Cape Region was, for a while, an island cut off from the rest of the peninsula by an arm of the sea that extended from the head of the present bay at La Paz to the Pacific. The former strait is now occupied by the southern portion of the Magdalena Plain which receives little rainfall. In contrast, the mountains of the Cape Region have a fair amount of precipitation and there is permanent water in many of the canyons. In these, and along the few intermittent streams flowing into the sea, *celaeno* finds a favorable habitat. Specimens have been collected at elevations up to 700 meters and the species very likely ascends even higher.

Geological evidence makes it clear that no transverse ridge has existed across the Gulf for a very long period of time, hence migration in the past by means of any land bridge may be ruled out. The close relationship of the two races of snakes cannot be denied, however, and it should be pointed out that almost everyone who has written on the fauna of Baja California has remarked about the great similarity between certain plants and animals of the Cape Region and their counterparts on the mainland.

The only logical explanation for such an anomalous distribution is to postulate a former much wider range for *Natrix valida* (considering the species as a whole) than now exists. If it could be shown that this snake once occurred much farther north—at least to the head of the Gulf (which formerly extended to the basin of the Salton Sea)—and was forced southward on both the mainland and the peninsula, then the reason for the present discontinuous distribution would be quite clear.

Such a situation may have existed. There are indications that our own Southwest and adjacent Mexico (including Baja California) received more precipitation during the Pleistocene than now. Hence there probably were

numerous habitats suitable for *valida* in much of what is now desert or semi-desert country. The increasing aridity of the post-Pleistocene may have destroyed such habitats, bringing about a southward displacement in range, one population surviving only in the Cape Region and the other maintaining itself in the more extensive and more favorable coastal plain of the mainland. Isolation has resulted in the development of differences, enough, at least, to make possible the recognition of the two populations as subspecies.

Some corroboration of the belief that *valida* once occurred much farther north is furnished by data published by Bogert and Oliver (1945) in their analysis of the herpetofauna of Sonora. They show (pp. 314-6) that thirty-seven (full) species of amphibians and reptiles (excluding marine forms) are known from both Sonora and Baja California. Of this number all but two also are found at the head of the Gulf, either in California or Arizona (or both), hence these many species exhibit present-day distributions that approximate the range which *valida* in all probability occupied in the recent past. If *valida* were known to occur in Sonora (it may be found in that state eventually, as stated above) then their list of species not now living north of the Gulf would be increased to three. Of these, one is *Ctenosaura hemilopha* which, since it is used as an article of food by the Indians of the region, may have been carried across by human agency. Significantly the other two—*Natrix valida* and *Pseudemys scripta* (subspecies *hiltoni* on the mainland and *nebulosa* on the peninsula)—are both aquatic; both belong to genera which are not well adapted for existence under arid conditions.

The survival of animals as relicts in peninsulas extending southward from continental masses has recently been discussed by Schmidt (1943). There are a number of other animals besides *celaeno* now living in the Cape Region of Baja California that are also obviously relicts.

It is of interest to call attention to the fact that *Natrix sipedon compressicauda* exhibits phenomena of distribution and coloration closely paralleling those of *celaeno*. It occurs in the southern part of another southward-extending peninsula (Florida) and it has a number of variations in color and pattern, just as has *celaeno*.

In relation to all other existing water snakes the two subspecies of *valida* occupy a well-isolated geographic position. Their nearest neighbors (of the genus *Natrix*) are *rhombifera* and *blanchardi*, which occur along the east coast of Mexico, and *transversa*, which enters some of the Mexican border states from the north. From them, however, *valida* is separated by high mountains, extensive deserts, or both, and it obviously bears no close relationship to any of them.

Relationships

In scutellation, dentition, and hemipenial characteristics *valida* agrees with other members of *Natrix* as that genus is currently defined. Yet it apparently has no close relatives among North American water snakes. From the larger kinds, such as *sipedon*, *erythrogaster*, *taxispilota*, and *rhombifera*, it differs by

lacking scale pits; from most of these it also differs in the shape of the head and in bodily proportions. Members of the *septemvittata* group, with their relatively small heads and their usually clean-cut striped patterns, also are quite different from *valida*. It is true that many specimens of the subspecies *celaeno* bear light-colored lateral stripes, but these markings are ragged and uneven, especially along their upper margins. The pattern of typical mainland *valida*, with its numerous small maculations on a nearly uniform ground color, is unique among New World *Natrix*. In certain respects this pattern is similar to that of some of the spotted Asiatic members of the genus, and it is possible that we may have to look across the Pacific Ocean for a clue to the relationships of *valida*. Perhaps the studies now being made upon Old World *Natrix* by Edmond Malnate may shed some light upon this possibility.

If *valida* had a single, instead of a divided, anal plate no one would hesitate to classify it in the genus *Thamnophis*. Its resemblance to the garter snakes is remarkable; its scales lack apical pits, many individuals bear light spots along the common suture of the parietals, and at least one specimen of *valida* (EHT-HMS 4982) is marked with a prominent light middorsal stripe. Spotted patterns are common in *Thamnophis* and several members of that genus bear markings which are similar to those of typical *valida*. Cope erred by identifying as *valida* a specimen of *Thamnophis ordinoides vagrans* from Utah that had an abnormal (divided) anal plate, and more recently Dunkle and Smith (1937, p. 3) mistook a *Thamnophis rufipunctatus* for *valida* (see p. 260). The melanistic phases of *celaeno* look like the darker kinds of garter snakes which have well-defined lateral stripes but no middorsal ones. Also the habits and habitats of *valida* and *celaeno* are similar to those of most of the western species of *Thamnophis*, although apparently they cannot exist under quite such arid conditions as many of the garter snakes.

Taking all these matters into consideration, the conclusion is obvious that *valida* must lie close to the ancestral line from which the genus *Thamnophis* developed. No one can deny that the two genera are very closely related. The only characteristic which will serve to distinguish them is the condition of the anal plate—divided in *Natrix* and single in *Thamnophis*. Some kinds of *Thamnophis*, notably *angustirostris*, look more like water snakes than garter snakes. In contrast, *valida* resembles a garter snake far more than it does any other North American water snake. The anal characteristic, although rather constant, does not always hold, for I have seen several specimens of *Natrix* with single anal scutes and a few of *Thamnophis* with divided ones. Instances are known in which both types of anal scutellation may occur in the same species (Grant, 1940, p. 50). For the sake of convenience it is highly expedient to retain the genus *Thamnophis* as distinct from *Natrix*, but *valida* comes close to being a link between the two.

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A Change from Grassland to Forest Vegetation in the "Big Barrens" of Kentucky*¹

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From historical literature came most of the material for this paper concerning the nature of the vegetation soon after that part of Kentucky known as "Big Barrens" was settled by the whites. Personal observations since early childhood and field work within recent years contributed the material relative to the forest vegetation which followed.

Location of the Barrens and the Prevailing Conditions

When the first white settlers came to Kentucky they found vast regions of grassland with only occasional trees, all of which had a stunted growth that made them unsuitable for building material, fences, and fuel. Most of the grassland was in the western half of the state and the main area, referred to as "Big Barrens," formed a narrow strip extending from the Ohio River about thirty-five miles west of Louisville southward to the Tennessee State line and westward to the Cumberland River. The estimates concerning the extent of surface of this particular grassland ranged from 5,000 to 6,000 square miles.



Map of Kentucky, showing the approximate location of the Big Barrens at the beginning of the nineteenth century.

For the most part, the grassland corresponded with that part of Kentucky having soil derived from a series of very soluble limestones composed of the Renault-Paint Creek, Ste. Genevieve, and the upper part of the St. Louis limestones. The prairie vegetation was not continuous, however, for in certain localities, especially along streams that traversed the area, there was a good growth of timber (Dicken, 1935a). Furthermore, there

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was a part of the Cypress sandstone of the Chester series included in this grassland, but the extent was not very great, and it was always on land having limestone only a very few feet below its surface.

The name "Barrens" was given to this region to describe the potential productivity of the land, for the pioneers thought that the absence of trees indicated that the soil was unproductive. These men had previously used trees as criteria regarding the fertility of the land—associating certain species with definite land quality—and when they reached this region which was destitute of trees, they obviously thought that the land lacked certain essential properties (McInteer, 1942).

According to the early writers, tall bluestem was the most common plant within the Barrens, but there were many others, including small and scattered individuals of oaks, hickories, willows, plums, hazel, buttonbush, sumacs, and wild grapes. Also, there were many herbs, some of which were goldenrods, asters, shooting star, Indian grass, prairie clover, compass plant, coneflower, gerardia, gall-of-the-earth, cudweed, and blazing star (Michaux, 1805; Owen, 1856; Garman, 1925). Gorin (1929) stated that in the spring, summer, and fall the Barrens were covered with millions of the most beautiful and variegated flowers. Michaux (1805) complained about the "doleful uniformity of these immense meadows." According to oral tradition, one could often ride for miles and not find a riding switch, and Owen (1856) stated that the old inhabitants declared that when that part of the country was first settled it was an open prairie with hardly a stick of timber of sufficient size to make a rail as far as eye could see. Undoubtedly this land had been destitute of trees for a long time, for the pioneers failed to see any evidence such as logs, stumps, or their charred remains to suggest that the land had produced trees of good size within recent times (Hussey, 1876).

The Vegetation of the Present Age

The region that was previously covered with prairie vegetation is now occupied with cultivated fields, pasture land, and forest vegetation. None of the wooded portions, however, have the nature of virgin forests such as those found in other parts of the state, for these species of trees cannot attain great size in the short time that has elapsed since the whites appeared and the Indians left the region. Only the original specimens of trees could be more than 150 years old and most of those have been cut by the farmers, because the timber was in great demand as soon as it became large enough to serve as building material. Most of the timber is either in wood lots or on land that is too uneven to be plowed.

The twenty species of trees that are most abundant in the region of the Barrens are Spanish oak (*Quercus falcata*), post oak (*Quercus stellata*), red oak (*Quercus borealis* var. *maxima*), red cedar (*Juniperus virginiana*), white oak (*Quercus alba*), black oak (*Quercus velutina*), sour gum (*Nyssa sylvatica*), shellbark hickory (*Carya ovata*), sugar maple (*Acer saccharum*),

persimmon (*Diospyros virginiana*), chinquapin oak (*Quercus Muhlenbergii*), red mulberry (*Morus rubra*), chestnut (*Castanea dentata*), pignut hickory (*Carya glabra*), white ash (*Fraxinus americana*), blackjack oak (*Quercus marilandica*), black walnut (*Juglans nigra*), white hickory (*Carya tomentosa*), tulip tree (*Liriodendron Tulipifera*), wild black cherry (*Prunus serotina*) (McInteer, 1941; Braun, 1943). This list includes twelve species with heavy fruits (oaks, hickories, walnut, chestnut), three with winged fruits, and five with fleshy fruits. Naturally one would expect migration to occur much faster among species with winged and fleshy fruits and then he would wonder why oaks, hickories, walnut, and chestnut are most abundant all over the region within less than a century and a half after the Indians left, at which time the prairie fires were lessened and the woody plants began to thrive. It was not a fact that these species had migrated faster than had the others. They were already there. These are the ones mentioned mostly by our early writers as being of small individuals scattered over the grassland. One explanation for this difference in the relative abundance of the trees at that time is that the large propagules of certain species were injured less by the prairie fires than were the smaller ones, thereby enabling the species to remain in spite of these conflagrations in the grassland.

Many of the wood lots appear to have been disturbed only a very little by the ax and saw, for they contain many trees large enough to make excellent saw logs. Not only is it true that saw mills are common in the region of original grassland, but I can recall having seen many of them in my early childhood, the time of which was only a little more than a century after that part of the state was settled. These mills were small (and still are, for that matter) and were operated only for local demand. Also, at a very early age, I helped clear timber from some of the land for cultivated crops and many of the observations and impressions have remained very clear. I, with my little ax, cut small trees while the men felled the larger ones. I thought that our largest trees were enormous, but when visiting relatives who resided outside the Barrens, I was impressed that our trees were not so large as theirs and this was quite a puzzle to me, for I could see that our land was more productive of cultivated crops. I did not know that our land had been covered with grass and that the trees were comparatively young. I knew, too, that our section of the country was referred to as "Barrens" but I did not realize the significance of the word.

Another item of interest to me to illustrate the age of these trees is that the annual rings of these felled trees were counted and rarely was one found to be more than a hundred years old which means that only a few of the individuals were there when this region was settled. The most common of these oldest trees were referred to by the men who were clearing the land as hickories, white oak, red oak, post oak. Perhaps the so-called "red oaks" were mostly Spanish oak, Eastern red oak, and black oak.

The wooded territory, taken as a whole, is fairly rich in number of species. That part which has its soil derived from the Cypress sandstone differs from that coming from the limestone in that each section has some common

species that are rare or entirely lacking in the other. Only the sandy soil has mountain laurel, sourwood, pine, scarlet oak, and cranberries. On the other hand, red cedar is abundant only on the limestone soil. In fact, on the south-facing slopes of Dripping Spring escarpment and outlying knobs a person can determine from a long distance the contact between these two geologic formations, for red cedars grow in abundance only up to the sandstone (McInteer, 1941).

Origin of these Types of Vegetation

Perhaps the students of plant ecology are more concerned about the causes of the two types of vegetation than in knowing the flora in the two periods of time. Since the region of the Barrens is so near the heart of the deciduous forest formation and since the trees have grown well for the last 150 years, it is reasonable to maintain that the usual climatic conditions here would be associated with the present vegetation but that something out of the ordinary must have been a factor in determining the peculiar plant growth found by the early pioneers. It may be difficult to offer an explanation for the treeless condition, followed by the development of the prairie vegetation, and the permanency of the grassland. The early writers, taken as a whole, indicated the location of the Barrens and the conditions that were prevalent when the region was first settled, and while they presented their own ideas, they did not express very clearly the real cause for such conditions, for that which was responsible for this situation dates much earlier than the time of the first pioneers of that part of Kentucky. Relative to the origin of the Barrens, consideration should be given to the natural causes which may be climatic, edaphic, or both, as well as biotic, including the practices of the men who had previously occupied the country.

A number of the early writers claimed that frequent fires were the cause of the prairie vegetation. Michaux (1805) explained that not only the Indians, but also the first white settlers made a practice of burning the grass of nearly every year to attract game into the open and to make better pasturage for the cattle and that this practice retards the growth of other plants. Both Shaler (1885) and Bourne (1820) likewise thought that the customs of the Indians were the main cause in bringing about this peculiar plant growth.

Sauer (1927) brought out the fact that there was a correlation between the area of the "cavernous limestones" and that of the grassland which at least suggests that there is a connection between the quality of the decomposed rock and the vegetation which it supports. On the other hand, Transeau (1935) maintained that certain factors of climate, especially humidity, were a great contributing cause to this grassland. He showed that the relative humidity is lower in that region (added to the Western Coal Basin) than in other parts of the state and he stressed that this low humidity is favorable to the development of prairie vegetation. This change in climate from place to place, however, is gradual and is not sufficiently pronounced to account

for all the variations in vegetation, which in this case correspond to the variations in the earth's crust relative to the underlying rocks.

The presence of prairie vegetation in that part of Kentucky could not be due to the average precipitation of the present age, for this ranges from 45 to 50 inches and this is above the minimum requirements for our forest trees. Nor could this type of vegetation be due to the distribution of rainfall during the growing season, for this is fairly uniform with March, the highest month, having approximately five inches and September and October the lowest months, each having about three inches on an average. No doubt this part of the world has experienced some extremely dry spells within the last few centuries and perhaps one of these was the first step in bringing about the conditions found in the Barrens.

Since the region of grassland so closely coincides with a narrow strip of land derived from those soluble limestones it seems reasonable to claim that the quality of the rock was a great contributing cause to the development of the prairie vegetation in a region surrounded by forests. Apparently, trees on land underlain by a thick, compact layer of limestone, from a few inches to several feet below the surface, cannot endure a drought as well as can the same type of plants on the other soils in that part of Kentucky.

The soil in such a geologic region becomes dry in a short time; for in the first place the run-off soon flows or seeps downward and drains away through the vast underground drainage system of streams moving in channels that have been formed by the action of ground water on the soluble limestone. There are no surface streams and true valleys are rare (Dicken and Brown, 1938). In the second place, water, by means of capillarity, could scarcely, if at all, move upward through the limestone layer, for it is practically impermeable to water (Dicken, 1935b). In addition, there is no definite water-table, for the water is all in the process of running away, but this is not the case on either side of the region of this soluble limestone. Furthermore, the roots of plants can penetrate sandy soil to a much greater depth than can be done in the compact clay that is common in most of the region of the Barrens. Shantz (1938) has brought out the fact that the soil conditions and vegetation are quite similar on sandy soil even though the rainfall may vary considerably. This is due to the water quickly draining from the sand allowing it to become well aerated in times of heavy rainfall and to its ability to retain available water at a great depth where it is protected from evaporation at a time of litter or no rainfall. Within the region are high hills or knobs which are outliers of the Cypress sandstone and they supported a compact growth of forest vegetation on the sandy soil in spite of the uneven topography which is generally associated with a great run-off during a heavy rain.

This condition of underground drainage does not exactly coincide with that part of Kentucky whose soil was derived from the soluble limestone, for it is also found in a part of the Cypress sandstone, especially in those sections in which the layer of sandstone above the Ste. Genevieve lime-

stone is not very thick, allowing the land to have that underground drainage system and this fact, no doubt, contributed to the cause of the grassland extending into the region of sandy soil at certain places.

The above paragraphs merely tell how the treeless condition was probably brought about, but fail to explain directly the presence of the prairie vegetation. After the land became treeless, grasses and other herbs migrated to and became established in the region as soon as conditions became favorable for their growth and reproduction. There were two sets of ideas relative to the land's remaining in grass. Some claim that certain factors of climate, especially the extremes, were favorable to the growth of grass by being unfavorable to the growth of trees—not on all land but on that which had tendency to be thirsty—and that this alone was sufficient to bring about and maintain conditions in the vegetation found by the early pioneers.

Many claim, however, that fires were the main cause, since fires which might entirely destroy annuals and woody plants could scarcely hurt the herbaceous perennials having underground stems from which shoots could readily grow. Much consideration should be given to their claims, for fires are much more effective in this limestone region than in other parts of the state, since, with few exceptions, there are no surface streams; they are mostly underground. When a fire is started under such conditions it meets with no natural barriers such as valleys and streams of water. The surface is uneven due to the presence of sink-holes but these would scarcely slow down a fire as would a valley. Since fires move slowly down a hill, a mere brook might stop it. No doubt there were times, especially in rainless seasons, in which fires swept the grassland for days, consuming all the dried plants on hundreds of square miles.

The whole explanation of the cause of the Barrens is complex. I am of the opinion that this grassland was due to the combined influence of the nature of the soil, the type of underlying rock, certain climatic conditions, and frequent fires and that as soon as these extremes in climate were less pronounced and the cultural practices of the inhabitants were altered, conditions became favorable for a rapid growth of forest vegetation.

Summary

1. The pioneers found vast regions of grassland in some parts of Kentucky.
2. The early settlers gave the name "Barrens" to the region, because they thought that the absence of trees signified that the land was low in productivity.
3. The "Big Barrens" formed a narrow crescent that corresponded to that part of Kentucky having karst lands, covering an area between 5,000 and 6,000 square miles.

4. It seems that the treeless condition was brought about by a severe drought, followed by the invasion of species of prairie plants, and that thereafter the grasses remained, due to the combined influence of the unusual conditions in the earth's crust, extremes in some factors of climate, and to frequent fires.

5. After the region was settled by the whites a young forest growth sprang up all over that part which shortly before had been covered with prairie vegetation.

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Shoot Segmentation in *Anacharis densa*

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Anacharis densa (Planch.) Vict. has passed under the name of *Egeria densa* Planchon, *Elodea densa* Caspary, *Elodea canadensis* var. *gigantea* (horticulture), as well as *Philotria densa* until 1931 when Marie-Victorin untangled the confusing nomenclature. *A. densa* is the most robust member of the genus and its reproductive vigor is quite in keeping with its size, but it will probably never have as colorful a history as that of *Anacharis canadensis* in England since it is not as hardy as that species. Its native habitat is the streams and lakes of southern Brazil to the delta of the La Plata in Argentine. In the United States it is commonly cultivated in aquaria, pools, and greenhouses but may occur locally (chiefly in the south and coastal states) as an escape where it may choke small ponds or sluggish streams.

Its mode of vegetative propagation (breaking up of the shoots) is similar to that of *A. canadensis* and its near kin, but *A. densa* appears to have at least one unique feature as compared with *A. canadensis*. This feature is the presence of a well developed region of breaking in the stem just above the origin of each lateral bud. Breaking is at random in *A. canadensis*. It would be of interest to know the behavior of other species.

Grier (1920) has shown that lateral buds occur only at certain nodes in *A. canadensis* and that stem fragments which do not contain buds are unable to regenerate the plant. This is also true in *A. densa*. Buds are uniformly arranged in *A. canadensis*, occurring usually at every ninth or tenth node. The nodes are otherwise just alike bearing usually three whorled leaves, but the lowermost ones may bear only two, and occasionally four occur. Fragmentation may take place anywhere but considerable tension or shearing is necessary. Lateral buds expand and grow readily on shoots with active terminal buds.

A. densa is similar in that its buds are also uniformly arranged, occurring at intervals of ten to fifteen nodes, but the shoot differs in its greater differentiation, including the segmentation region in the internode just above each lateral bud. This feature and others give a well marked segmental structure to the shoot. At maturity only slight bending tension is required to cause separation of the segments (fig. 1), which themselves are very flexible and difficult to break. The major portion of each segment is composed of internodes separating a series of similar nodes bearing usually four, but frequently only three, and sometimes five leaves. Microscopic examination of longitudinal sections discloses a nodal diaphragm of closely-packed isodiametric cells separating adjacent internodes. The diaphragm has only a few small intercellular spaces. It is one to three or several cells in thickness (fig. 5). Numerous tubular lacunae extend the length of the internode. The distal portion of each segment is unique in several respects. No internode develops between the last two nodes



FIGURES 1-6.—*Anacharis densa*. 1. A portion of a shoot that has undergone segmentation at each brittle region, $\times 2/5$. Note that all buds are still inactive. 2. Development of lateral buds on a shoot that has been decapitated by segmentation, $\times 2/5$. 3. An active segment with young shoot and young adventitious root, $\times 3/4$. 4. Longitudinal section through distal portion of a segment showing broken end, one ordinary node, and the double node with one large and one very small lateral bud, $\times 10$. 5. Longitudinal section through the single nodal diaphragm of an ordinary node, $\times 70$. 6. Longitudinal section through the double diaphragm of a double node, $\times 70$. Note lacunae separating the diaphragms.

so that two whorls of leaves occur at this point (fig. 3) giving eight when the lower nodes bear four leaves, and six when the lower nodes bear three leaves each. It is at this double node that the lateral bud is borne. Separation of the segments occurs near the base of the next higher internode (fig. 4).

Through microscopic examination of sections various anatomical features relating to the mode of propagation being discussed here were observed. I am indebted to my wife for aid in preparation of the sections used. The material was fixed in FAA, embedded in paraffin according to the Craf schedule, sectioned at sixteen micra, and stained with safranin and fast green.

Segmentation was found to involve breaking of the cell walls (fig. 4) and not their separation. It occurs through any of the cells in the region of breaking, not through specific cells. This region occupies the lower one-third of the internode and its cells differ from other internodal cells in containing very few starch grains and possessing thinner walls. The stem is usually noticeably swollen here. It is possible that the low starch content is correlated with high sugar content and correspondingly a high turgor pressure, which together with thin, non-elastic, mature cell walls would account for the brittle structure observed. The importance of turgor pressure is further indicated by the rapid loss of brittleness in killing fluids. Within a few hours after placing shoots in FAA they may be bent sharply at the segmentation region without breaking.

The double node from which the lateral buds arise was found to have a double diaphragm (fig. 6). Its two components are separated by a single layer of lacunae. Thin walled spiral vessels were observed running through the nodal tissue from the vascular column into the lateral bud. In addition to the large bud, one or more small shoot primordia (fig. 4) and a root primordium are commonly present. It is questionable whether these structures could all arise from so small a mass of undifferentiated parenchyma as is present at the single nodes. This viewpoint is further strengthened by the occurrence of flowering spathes at similar double nodes.

Lateral buds rarely expand and grow unless the terminal portion of the shoot is lost (fig. 2) or segmentation occurs (fig. 3). Root primordia may elongate either before or after segmentation.

Segmentation may begin four or five segments back from the shoot apex. The region of segmentation does not become brittle, and so is not functional at low intensities. For this reason it is rarely observed in aquaria. The lower segments which may develop in deep water also lack brittleness for the same reason. The material from which the foregoing data were obtained was grown in a greenhouse pool exposed to good direct sunlight and moderate temperatures (14° - 20° C.). Segmenting stems have been observed at all seasons.

Due to the ballast of lime, small aquatic animals and epiphytic algae which accumulate on the older portions of the shoot, the segments usually drop to the bottom after breaking apart. That the segments are still buoyant is readily shown by rubbing off the debris, after which they rise to the surface of the water. Weighting of the shoots in this manner apparently performs a useful

role in the economy of the plant. Segments which resume growth while resting on the substratum send their roots into a richer mineral nutrient reservoir than they would if they were floating. Then too they might be washed onto dry shores more easily if floating. The young shoots, which have not had time to accumulate ballast, rise erect in the water and quickly reach the surface. The large starch reservoir in the segment and increased length of internodes under weak light are important features in the development of young shoots since photosynthesis would proceed at a very slow rate until the new shoot had risen above the bottom litter into the clearer water.

Summary

1. *Anacharia densa* propagates vegetatively by means of well differentiated shoot segments.
2. Each segment is made up of ten to fifteen nodes of which the most distal two are united without an internode.
3. Only the double node gives rise to lateral buds and adventitious roots.
4. Cell walls are broken during segmentation.
5. Breaking occurs in the lower one-third of the internode just above the double node.
6. The cells of this region are thinner walled and contain fewer starch grains than those in the remainder of the segment.
7. Breakage at this point is probably due to a combination of weakness and low flexibility caused by high turgor, and thin rigid walls.
8. High light intensity is essential in the formation of brittle regions of breaking.
9. The accumulation of lime as well as plant and animal organisms on the older portions of shoots forms a ballast which causes the segments to sink.

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Book Reviews

AN INTRODUCTION TO THE TAXONOMY AND NOMENCLATURE OF FUNGI. By G. R. Bisby. Imperial Mycological Institute, Kew, Surrey, England. vii + 117 pp. \$1.25.

The increasing recognition of the importance of fungi, not only in plant pathology, soil microbiology and other phases of agricultural sciences, but in medicine and industry, calls for an improvement in the basic mycological training of those who plan work in any of these fields as well as those who desire to learn more about the fungi as living organisms of great interest in their own right. Bisby's work places in the hands of students and instructors a valuable means to that end. The first portion of the book is devoted to introductory material and taxonomy, including concise discussions of equipment, methods of examination, recording of data and publishing and illustrating. A short chapter "To the Amateur" and remarks elsewhere to the same address indicate that the author hopes that the revival of interest in systematic mycology will continue to spread beyond professional circles.

The second part deals with nomenclature. The bulk of it, constituting almost half of the entire book, comprises the text of the International Rules of Botanical Nomenclature. This is not a mere reprint of the official 1935 edition but incorporates the changes made at Amsterdam in 1935, not, so far as the reviewer is aware, heretofore codified in this way. An even more useful modification from the standpoint of mycologists is the substitution of examples selected from the fungi instead of the phanerogams to illustrate the application of the Rules.

This book should be accessible to every serious student of the fungi. Experienced mycologists will find the treatment of the Rules, even though unofficial, more convenient than that in the official edition and should have no difficulty in distinguishing between what is required to conform to them and what is the present author's interpretation, and few can read the first portion without finding useful suggestions. The few typographical errors noted are unimportant. It may be expected that the book will have the wide circulation warranted by its merits.

—G. W. MARTIN.

FUNGICIDES AND THEIR ACTION. By James G. Horsfall. The Chronica Botanica Co. Waltham, Massachusetts; G. E. Stechert and Co., New York. 1945. 239 pp., 24 figs. \$5.00.

The object of this book, as stated in the preface, is to discuss the materials used for killing plant pathogens, considered in the light of the chemistry and physiology of toxic action, and the problem of delivering such materials where they are most effective, with special reference to the mechanics of application. A brief historical survey is followed by a discussion of general concepts and methods of laboratory assay. The chapter on treatment of data stresses the usefulness and significance of the straight-line dosage-response curve. The mechanics of treatment occupies four chapters, discussing deposition, coverage of single surfaces, coverage of multiple surfaces and tenacity. The recent significant work on artificial immunization and chemotherapy is reviewed and it is suggested that the former may be expected to become increasingly important. The action of copper, sulphur and organic compounds is discussed at some length, and chapters on antagonism and synergism and on toxicity complete the text, which is followed by a bibliography of approximately five hundred titles and complete general and author indexes.

The style is clear and vigorous, sometimes to the point of being a bit startling, and the author's sense of humor and impatience with pedantic stuffiness has occasionally betrayed him into curious locutions. One need not be a stickler for avoidance of terminology to wonder whether it is necessary to say what *Phytophthora infestans* hopes to do and it may be questioned whether introduction of chemicals into a plant makes the

plant feel better. Cliches which might pass with little notice are unduly emphasized by quotation marks. But as a whole, and especially considering the astonishing amount of technical information included, the book is eminently readable. No attempt is made to give detailed directions for the control of specific diseases but emphasis throughout is on the basic principles involved. Primarily addressed to plant pathologists, those who are interested in insect control and in the protection of inert materials such as wood or textiles will find the volume a mine of information and a stimulus to research.

—G. W. MARTIN.

HOW TO KNOW THE MOSSES. By Henry S. Conard. H. E. Jacques, Mt. Pleasant, Iowa. 1945. 166 pp., 363 figures. Spiral binding, paper, \$1.50; cloth, \$2.50.

Dr. Conard has done an amazingly clever job in this little book. It is written primarily for the amateur and beginning student of mosses and liverworts, and will certainly go a long way to encourage an interest in these groups of plants. There is an introduction and a brief discussion of the characters of mosses, their life-history, habitats, uses, and classification; and a more detailed explanation of how to study mosses and liverworts, methods of collecting, equipment, herbarium, reference works, etc.

The bulk of the book is a picture key to the mosses and liverworts, of which approximately 400 and 100 species, respectively, are included. The genera and most of the species are illustrated to bring out the diagnostic characteristics. The drawings, most of which were made by Miss Louisa Sargent, are clear and concise and serve their purpose well. A few remarks on distribution, habitat, and closely-related forms complete the treatment of the species. The book is sure to do much to provide a happier excursion into the realm of liverworts and mosses..

—MARGARET FULFORD, University of Cincinnati.

THE AMERICAN NATURALIST. A Semi-Monthly Journal Devoted to the Advancement of the Biological Sciences. Edited by Jaques Cattell. Lancaster, Pa., The Science Press. Volume LXXX, No. 786, pp. 1-96, 1946. Institutional subscription, \$6.00; individual subscription in the United States, \$4.00.

When the oldest biological journal in the United States appears in a new vestment and its editorial policy is undergoing radical changes, this event is of singular importance to all biologists. Judging from the majority of letters sent by many distinguished subscribers in response to the editor's announcement of his plans late in 1945, the new *American Naturalist* apparently is being welcomed with open arms. Although still in its formative stage, the Editor hopes to formulate the new policy in the near future.

This issue, like all large issues scheduled for the first of each month, is made up of two sections; the first, set in smaller type and double column pages, contains an Editorial, Letters to the Editor on the Change in Policy, two short general articles, obituaries of three distinguished biologists, reports of the awarding of two distinguished medals, news of various appointments, Short Notes, and Book Reviews; the second Section on Genetics and Evolution (pp. 45-96) appears in its familiar form and, in twelve issues, will contain as many words per year as in the past. The next number to come, like all others scheduled for the fifteenth of every month, will be a 16-page news issue. To accommodate this increase in page number and broadening of the scope of the journal, the present subscription list must be multiplied at least five times. It is hoped that biologists will respond in sufficiently large numbers to materialize these plans and maintain the new policy.

Perhaps the *American Naturalist* is thus destined to become the official organ of all biologists who have not yet acquired a class consciousness equal to that of their colleagues, the chemists. If the diverse work, views, professional interests and common problems of all biologists can be integrated in this way, the result will amply justify the momentary risk and effort expended toward that noble end.—THEO. JUST.

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